PALEOBIOLOGÍA DEL LINAJE NEANDERTAL: PALEODIETA Y MARCADORES DE ACTIVIDAD EN LA DENTICIÓN DE LOS FÓSILES HUMANOS DE LA CUEVA DE EL SIDRÓN (ASTURIAS).

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A mi familia, en todo su sentido.

A Amanda y a Ainhoa.

A todos los que alguna vez han mostrado interés
en saber quienes fueron los Neandertales.

A ellos.

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Estalrrich, A., Rosas, A., García-Vargas, S., García-Tabernero, A., Santamaría, D., de la Rasilla, M., 2011. Brief Communication. Subvertical grooves on interproximal wear facets from the El Sidrón Neandertal dental sample. American Journal of Physical Anthropology, 144: 145–161.

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Dean, M. C., Rosas, A., Estalrrich, A., García-Tabernero, A., Huguet, R., Lalueza-Fox, C., Bastir, M., de la Rasilla, M., 2013. Longstanding dental pathology in Neandertals from El Sidrón (Asturias, Spain) with a probable familial basis. J. Hum. Evol. 64, 678–686.

Capítulo VI - División del trabajo en un grupo neandertal. Separación de tareas según sexo y edad.

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Capítulo VII - La dieta de un grupo Neandertal.

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Estalrrich, A., Rosas, A., (manuscrito enviado). Diet of a Neandertal Group: Occlusal Molar Microwear Texture Analysis of the El Sidrón (Asturias, Spain). Journal of Human Evolution.

RESUMEN

Esta tesis aborda el estudio del comportamiento biocultural de individuos de *Homo neanderthalensis* mediante el análisis de los datos obtenidos del su desgaste dental y su distribución en función de su sexo y edad. Tales datos se interpretan a la luz de la información y etnográfica disponible sobre el comportamiento de sociedades de cazadores-recolectoras. La base del estudio reside en la obtención de datos originales de los individuos del importante yacimiento de Neandertales de la cueva de El Sidrón (Asturias) y su comparación con datos originales de la grotte de l'Hortus (Francia) y grotte de Spy (Bélgica), así como datos bibliográficos. Igualmente, y con el fin de disponer de un marco amplio de comparación, se han obtenido datos originales de grupos cazadores-recolectores del Paleolítico Superior de la cueva de la Paloma (Asturias) e Indian Knoll (Kentucky, EEUU), y datos provenientes de fuentes bibliográficas.

Este trabajo abarca un amplio espectro de rasgos del desgaste dental, tanto el relacionado directamente con la dieta a través del análisis fractal de la microtextura del esmalte dental en la cara oclusal (MTA), como el relacionado con el uso de la dentición anterior como una tercera mano (estrías culturales y melladuras en el esmalte dental), y participa en el análisis del cálculo dental y de las patologías bucodentales. Los resultados se estructuran en cuatro capítulos e incluyen siete artículos originales publicados (o en fase avanzada de publicación) en revistas internacionales *peer-review*.

En primer lugar se ha determinado que en la muestra de Neandertales proveniente de la cueva de El Sidrón está representado un Numero Mínimo de 13 individuos, de diferentes edades y ambos sexos (3 hombres, 3 mujeres y un alofixo adultos; 3 adolescentes, dos masculinos y uno posiblemente femenino; dos juveniles y un infantil. Esta identificación, junto con la determinación del sexo de alguno de los individuos por criterios genéticos (Lalueza-Fox *et al.*, 2011, en la que la doctoranda es coautora; *PNAS* 108: 250) sirve de base para los posteriores análisis.

Los estudios realizados en los rasgos del desgaste dental no masticatorio han mostrado el desarrollo de una división sexual del trabajo en los grupos Neandertales, donde las mujeres pudieron realizar actividades relacionadas con el raspado y preparación de pieles, y los hombres pudieron dedicarse al retoque del filo de herramientas líticas. También se ha visto que, independientemente de su edad, todos los individuos de un grupo utilizaban su boca como una tercera mano, y que además eran diestros, con un patrón de lateralidad manual moderno.

Por otra parte, el análisis fractal de la superficie oclusal de los molares muestra que la dieta de los Neandertales de El Sidrón incluía carne y vegetales (apoyado por la presencia de granos de almidón en su sarro), pero que la de las mujeres Neandertales era más abrasiva que la de los hombres, una diferencia que no se ha encontrado en las poblaciones cazadoras-recolectoras estudiadas del Paleolítico Superior de la cueva de la Paloma (Asturias) e Indian Knoll (Kentucky, EEUU), y que puede estar relacionada con la utilización de la boca por parte de las mujeres para ayudarse en la preparación de las pieles. Así mismo, se

han encontrado restos de plantas medicinales en el cálculo dental de estas mujeres. Tales diferencias podrían estar también relacionadas con la división sexual del trabajo antes apuntada.

Finalmente, de entre todos los individuos de la cueva de El Sidrón destaca un adulto masculino que es el único que presenta una grave patología dental. Al mismo tiempo, muestra patrones únicos en la distribución del desgate dental tanto masticatorio como no masticatorio. Estos datos, unido a al hallazgo de bitumen en su cálculo dental le confiere un comportamiento más especializado que el resto de su grupo.

Los resultados de estos estudios añaden evidencias acerca del comportamiento biocultural de los Neandertales, contribuyendo a mejorar el conocimiento que tenemos acerca de los roles que los individuos de esta especie tenían dentro de su grupo y cómo utilizaban los recursos naturales de los que disponían.

CAPÍTULO I - INTRODUCCIÓN

I.1 Enunciado de la Tesis.

Esta es una tesis sobre Paleontología Humana, en la que se han estudiado aspectos de la expresión del comportamiento, capacidades cognitivas y culturales en un grupo de *Homo neanderthalensis* del Pleistoceno superior a través del estudio de sus restos biológicos. Mediante el análisis del desgaste dental producido durante la masticación de los alimentos, y el desgaste dental al realizar actividades relacionadas con uso de la dentición como tercera mano, su expresión en los individuos del grupo, la variación de estos rasgos en las diferentes etapas ontogenéticas de esta especie, comparado tanto con otros individuos Neandertales como *Homo sapiens*, se han inferido características del comportamiento y capacidades cognitivas de esta especie extinta.

Al igual que ocurre con *Homo sapiens*, la historia biológica de *H. neanderthalensis* ha obedecido tanto a su evolución biológica como cultural. Conocer ambas es esencial para poder entender la especificidad de este grupo, y en esta tesis se presenta, desde un punto de vista biocultural, cómo y qué hacían estos humanos que habitaron Eurasia durante más de 200.000 años.

I.2 Modelos bioculturales: interfaz entre biología, ambiente y cultura. Marco teórico en el que se encuadra esta tesis.

Según el Diccionario Cambridge de Biología Humana y Evolución, *Homo sapiens* es una especie perteneciente al orden *Primate* (parvorden *Catarrhini*, familia *Hominidae*) que posee una tecnología o cultura que le permite ocupar ecosistemas que de otra manera sería imposible (Boyd y Richerson, 1985). Además, se caracteriza por tener una organización social extremadamente compleja. A diferencia de los demás organismos vivos, los seres humanos tienen una historia evolutiva que es la combinación de la evolución biológica y cultural, y eso es esencial para poder entender y conocer tanto su origen y especificidad, como los roles que desempeñan en los ecosistemas terrestres.

La variabilidad humana actual se debe a la capacidad de respuesta y adaptación al ambiente, donde los ambientes socio-culturales juegan un papel muy importante (McElroy, 1990; Tomasello, 1999; Huruschka *et al*., 2005; Richerson y Boyd, 2005; Dufour, 2006; Khongsdier, 2007). Una aproximación biocultural se caracteriza por tratar a los humanos como seres biológicos, sociales y culturales en relación con el ambiente que ocupan (McElroy, 1990).

Los modelos bioculturales tratan de entender o explicar la variabilidad humana mediante la relación entre los distintos componentes de un mismo sistema (biología, cultura y el ambiente tanto biótico como abiótico) en el que se estudia un elemento (características biológicas, etológicas o psicológicas de una población humana). El uso de los modelos bioculturales en el campo de la antropología biológica enlaza con los modelos de variabilidad, que tratan de explicar la variación biológica humana a través de la interacción entre humanos

y medioambiente, añadiendo el factor "cultura" a la ecuación (Khongsdier, 2007), tratando de entender las adaptaciones que se han producido a lo largo de la historia evolutiva humana. En este marco, se entiende como "adaptación" la característica de una estructura, función o comportamiento que permite a un organismo vivir y reproducirse en un ambiente determinado (Dobzhansky, 1970).

Así, el principal modelo propuesto es el Modelo general de adaptabilidad (*General Adaptability Model)*, desarrollado para entender en líneas generales la adaptación humana. Sirve para entender las relaciones de retroalimentación más sencillas (Thomas *et al*., 1989). Consta de 4 partes principales:

1. Componentes o factores abióticos: clima, altitud, recursos energéticos....
2. Componentes o factores bióticos: predadores, patógenos.....
3. Ambiente cultural: comportamiento, cambios sociales, cambios tecnológicos....
4. Variación humana: características morfológicas, genéticas, fisiológicas, demográficas, funcionales....

Este modelo propone un marco conceptual en el que la variación biológica humana es dependiente del ambiente (biótico y abiótico) e interdependiente del ambiente cultural, a su vez también está relacionado con el ambiente (Figura I.1).

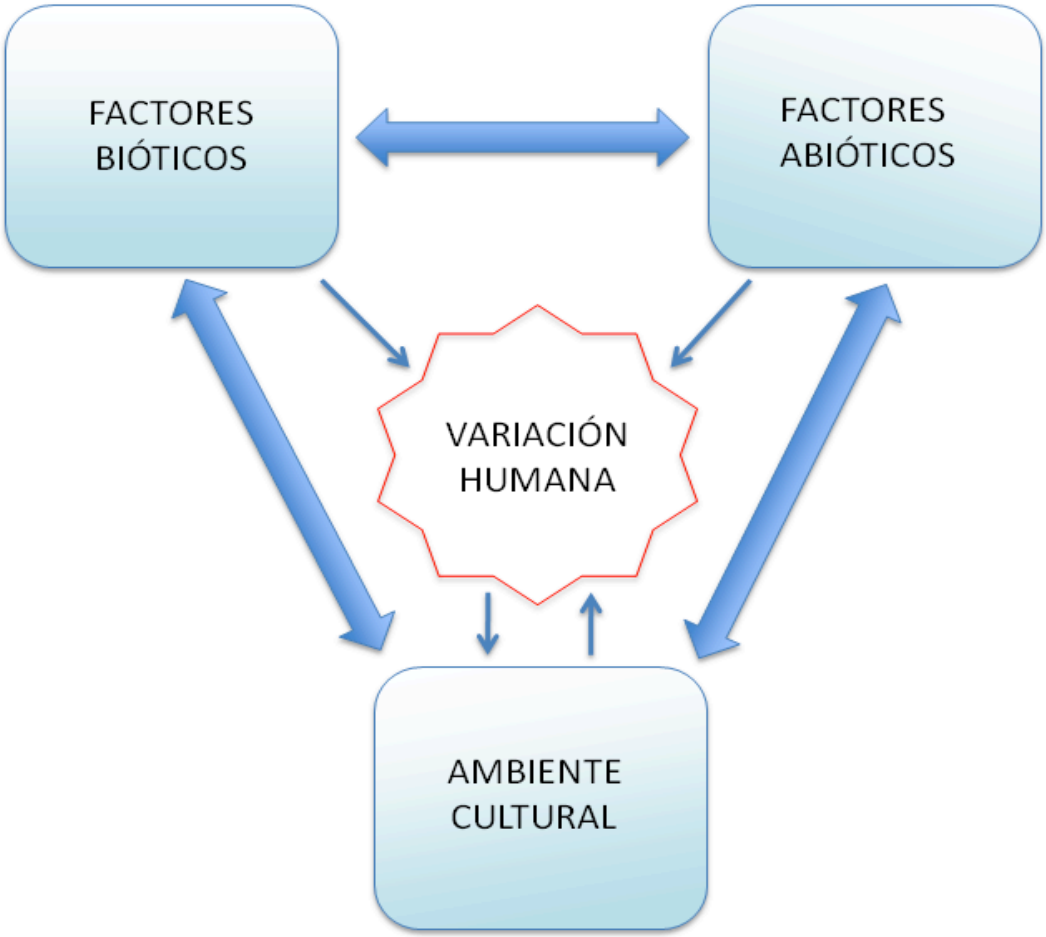

Figura I.1. Esquema de la relación entre el ambiente cultural, el ambiente físico, la biota acompañante y la variabilidad humana (modificado de Khongsdier, 2007).

A partir de este modelo, se han ido desarrollando otros, según se han considerado uno o varios factores. En 1960, Sherwood L. Washburn propuso el **Modelo de retroalimentación biocultural** (*Biocultural Feedback Model*), señalando que la cultura ha acelerado el proceso adaptativo de los primeros homínidos, y que los genes que favorecieron su desarrollo fueron seleccionados, lo que a su vez permitió más adaptación cultural, y selección de nuevos genes. Este proceso se habría repetido varias veces a lo largo de la evolución humana. En 1871 Charles Darwin publicó "El origen del hombre y la selección en relación al sexo" (en inglés el original *The Descent of Man, and Selection in Relation to Sex*),

sugiriendo que los humanos evolucionaron desde un ancestro común africano, un simio, que a su vez fue también el ancestro común de gorilas y chimpancés. Además, dijo que la reducción dental, el bipedalismo y el incremento en el tamaño del cerebro que se aprecian en los homínidos evolucionaron juntos gracias a un mecanismo de retroalimentación positiva en el que el uso de herramientas era el catalizador principal (Mai *et al*., 2005). Pero hoy, gracias al estudio al registro fósil, sabemos que los primeros homininos bípedos datan del Mioceno en torno a 4,4 M. a. (White *et al.*, 2009), mientras que el incremento del volumen cerebral comienza a ocurrir en el Pleistoceno, alrededor de hace 2 M. a. (Ross y Hennenberg, 1995; Ruff *et al*., 1997; Falk, 2000; Bruner, 2004; Rightmire, 2004; Holloway, 2008).

I.3 Evolución del género *Homo*: la cultura como nicho ecológico durante el Pleistoceno. La importancia de los dientes para el estudio de los comportamientos culturales.

La evolución, el cambio, es una característica poblacional (Mayr, 1997) donde la unidad evolutiva básica es el ciclo de vida (Bogin, 1997) porque es donde podemos observar la supervivencia diferencial de la variabilidad expuesta frente a una presión de selección impuesta por el ambiente.

En el caso del género *Homo*, "fue el bipedalismo lo que introdujo al hombre en su carrera evolutiva única. Pero el uso de herramientas estuvo presente igual de temprano.... Las herramientas cambiaron por completo el patrón de vida [del hombre], comenzando por la caza, cooperación y la necesidad de comunicarse y de un lenguaje.... En un sentido muy real, las herramientas crearon a *Homo sapiens*" (Washburn, 1960). Y es esa cultura la que ha permitido que *Homo sapiens* sea una especie cosmopolita, permitiendo que colonice espacios para los que sus características biológicas no están adaptadas (Boyd y Richerson, 1985; Castro y Toro, 2004).

Cada especie descrita en el proceso de evolución humana se ha asociado a un conjunto de industria lítica (Washburn, 1960; Brace, 1964; Leroi-Gourhan, 1964; Clarke, 1968; Wood y Richmond, 2000; Ambrose, 2001; Laland *et al*., 2001; Domínguez-Rodrigo *et al*., 2005; Richerson y Boyd, 2005; Toth y Schick, 2006; Gibbons, 2009), que a su vez forma un entramado sociobiológico (Wilson, 1975). En este nicho bio-socio-cultural, es donde las especies humanas se han desarrollado (Brace, 1964).

Los cambios biológicos que se fueron desarrollando, como la extensión de la etapa ontogenética inmadura o pre-adulta (Bogin, 1997; Bogin y Smith, 2012; Bogin *et al*., 2014), y una post-reproductiva cuyo origen se explica por la necesidad de procurar cuidados a la descendencia durante esas nuevas etapas de crecimiento (O'Connell *et al*., 1999; Álvarez, 2000; Kaplan *et al*., 2000; Hawkes, 2003, 2004), el incremento cerebral (Dart 1953; Washburn 1960; Aiello & Wheeler, 1995; Ross y Hennenberg, 1995; Ruff *et al*., 1997; Falk, 2000; Eaton e*t al*., 2002; Antón, 2003; Bruner, 2004; Holloway, 2008; Rightmire, 2013) y modificación de las proporciones corporales hasta las del hombre actual (Arsuaga *et al*., 1997; Antón, 2003; Rightmire, 2008), que favorecieron la migración humana fuera de África y expansión por el planeta (Gabunia *et al*., 2000; Goren-Inbar *et al*., 2000; Bar-Yosef y Belfer-Cohen, 2001; Roche *et al*., 2003; Pappu *et al*., 2011; Lordkipanidze *et al*., 2013; Vallverdú *et al*., 2014), o el cambio en la dieta más especializada en tubérculos, nueces, semillas o raíces (Kay, 1985; Grine y Martin, 1988; Teaford y Ungar, 2000; Grine *et al*., 2006; Ungar *et al*., 2006; Ungar *et al*., 2008) hacia una dieta más amplia, en la que se incluiría también carne (Rose y Marshall, 1996; Bunn, 1994, 1997; Milton, 1999; Domínguez-Rodrigo *et al*., 2005, 2010; Pontzer *et al*., 2011; Saladié *et al*., 2011; Yravedra *et al*., 2012; Huguet *et al*., 2013), entre otros, fueron determinantes en el establecimiento de relaciones interpersonales entre los individuos, cada vez más complejas, y del desarrollo de nuevos comportamientos culturales.

Por ejemplo, el desarrollo de nuevas etapas en la ontogenia (niñez y adolescencia), permitió, entre otras cosas, acortar el intervalo entre los nacimientos de los hijos (Ellison, 1990). No está claro cómo ha aparecido esta

etapa, pero si que ha debido necesitar que los individuos desarrollaran algún tipo de estrategia comunes o grupales para poder cuidar y alimentar a los niños durante su desarrollo (Burkart *et al*., 2009; Bogin *et al*., 2014), evidenciando otra vez que la relación entre los factores biológicos y culturales están estrechamente ligados en la evolución del género *Homo*.

La caza o el carroñeo responsable del aporte cárnico y signo del cambio en la alimentación ocurrido durante el curso de la evolución humana, tiene otro matiz más ya que además incrementa la complejidad interpersonal y social, y el cambio en los patrones de subsistencia jugó un papel importante en el desarrollo de la división del trabajo y de los recursos compartidos (Washburn y Lancaster, 1968; Isaac, 1978; Milton, 1987). La dieta es determinante en la ecología de las especies y en su comportamiento, siendo tal que la disponibilidad de recursos es capaz de determinar el tamaño del grupo, patrones de movilidad y la organización social (Hladik, 1975; Fleage, 1999; Grine *et al*., 2006). El conjunto de dientes y mandíbulas es el responsable de procesar los alimentos que se ingieren, son capaces de rebanar, sujetar, cortar y moler, y además en el caso de los primates, y particularmente en el género *Homo*, se usa la dentición anterior como tercera mano para ayudar en tareas como pelar y preparar frutos para comer, el curtido de pieles, sujetar diferentes objetos, etc. Y todas y cada una de estas actividades van produciendo una reducción en la altura de la corona dental y adelgazamiento de la capa de esmalte, conocido como desgaste dental (Molnar, 1972; Puech, 1979; Brothwell, 1981; Puech, 1981; Ubelaker,1989; Kelley y Larsen, 1991; Scott y Turner, 1997; Bax y Ungar 1999, entre otros). Así como los dientes varían entre los individuos de la misma especie en el tamaño de la

corona o pequeños detalles en el desarrollo de las cúspides, el grado de desgaste del esmaltes dental, la intensidad y las diferentes tipologías del desgaste, como es lógico, también varían dependiendo del uso que los propios individuos les hayan dado.

Por todas estas razones, por toda la potencial información y variabilidad tanto biológica como cultural que los dientes tienen, son considerados como unas piezas fundamentales para el estudio del registro fósil de la evolución humana y por eso se han seleccionado como muestra de estudio en esta tesis.

I. 4 *Homo neanderthalensis* (King, 1864).

Eran cazadores activos y carnívoros especializados en mamíferos de talla media y grande (Gaudzinski y Roebroeks, 2000; Hoffecker y Cleghorn, 2000; Patou-Matis, 2000; Richards *et al*., 2000; Pérez-Pérez *et al*., 2003; Bar-Yosef, 2004; Bocheners *et al*., 2005; El Zaatari *et al*., 2011). También se sabe que aprovechaban recursos marinos, que cazaban pequeños animales, vegetales y tubérculos y que además, cocinaban la comida (Stringer *et al*., 2008; Henry *et al*., 2011; Blasco *et al*., 2012; Hardy *et al*., 2012). Respecto a su comportamiento, se sabe que tenían un gran conocimiento del medio natural en el que vivían (Henry *et al*., 2011; Hardy *et al*., 2012), que fueron capaces de adaptar y cambiar su cultura material (Caron *et al*., 2011; Hublin *et al*., 2012), que la mayoría de ellos eran diestros (Bermúdez de Castro *et al.*, 1988; Lalueza-Fox y Frayer, 1997; Frayer *et al.*, 2010; Uomini, 2011; Volpato *et al*., 2012; Estalrrich y Rosas, 2013), que usaban pigmentos y plumas para su adorno personal (Soressi y D'Errico, 2007; Zilhão *et al*., 2010; D'Errico *et al*., 2010; Roebroeks *et al*., 2012), enterraban a los muertos (Solecki, 1975; Valladas, 1987; Gargett, 1989; Rendu *et al*., 2014) la distribución por áreas de actividad y los patrones de ocupación en las zonas que habitaban (Vallverdú *et al*., 2012), que la patrilocalidad era el patrón de residencia postnupcial (Lalueza-Fox *et al*., 2011) y que usaban plantas medicinales y bitumen para enmangar lanzas o hachas (Hardy *et al*., 2012).

A partir del estudio de los restos óseos de los Neandertales, bien por la morfología de los huesos (Dutour, 1986; Ruff, 1987; Lieberman, 2002; Villote *et al*., 2011), y junto con los datos que ha aportado el registro arqueológico, se sabe que tenían unos patrones de movilidad similares a los cazadores recolectores

actuales, aunque su comportamiento difiere en un punto esencial: no se han encontrado pruebas de una división sexual del trabajo tan especializada como la que aparece en *Homo sapiens* (McBrearty y Brooks, 2000; Kuhn y Stiner, 2001; 2006; Blasco *et al*., 2012; Cochard *et al.*, 2012). Es decir, según estos autores, tanto los hombre como las mujeres, y en ocasiones los niños, debieron participar en la mismas tareas, por ejemplo a la hora de cazar, el grupo al completo debía ir a cazar.

Respecto a su ciclo vital, varios autores (Smith y Tompkins, 1995; Macchiarelli *et al*., 2006; Ponce de León *et al*., 2008) sugieren que se componía de las mismas fases que el de *Homo sapiens*, es decir: infancia, niñez, etapa juvenil, adolescencia y etapa adulta. Aunque la duración de la niñez parece ser menor (Smith *et al*., 2007, 2010).

Durante el Pleistoceno superior es cuando *Homo neanderthalensis* alcanza su máxima expansión geográfica (Hublin *et al*., 1995; Zilhão, 1998; Shea, 2003; Finlayson *et al*., 2006; Rosas *et al*., 2006; Krause *et al*., 2007) y también cuando desaparece del registro fósil en torno a hace 40,000 años, pero varía según la localidad (Higham *et al*., 2014).

CAPÍTULO II - OBJETIVOS DE LA TESIS

Como se acaba de exponer, el incremento cerebral y de las capacidades cognitivas de *Homo*, le permitió desarrollar nuevas herramientas. A su vez, la implementación de las herramientas facilitaron el acceso a nuevos recursos energéticos, lo que permitió colonizar y explorar nuevos territorios, disponer de más recursos, que se pudieron reinvertir en el crecimiento cerebral, y otros cambios biológicos, y durante el proceso se ha incrementado la complejidad interpersonal y social, cambiando los patrones de subsistencia.

Así se forma un círculo de retroalimentación, ya descrito por Washburn en 1960, entre la evolución cultural y la evolución biológica en el género *Homo*, cuya representación actual se encuentra en la especie *Homo sapiens*, el complejo cultural, etológico y tecnológico que lleva asociado.

A la luz de este marco teórico, **se ha planteado el objetivo principal de conocer los comportamientos bioculturales en relación con la edad y el sexo de los individuos de *Homo neanderthalensis*.**

Este objetivo se ha abordado, a través el estudio del comportamiento mediante el análisis microscópico de los marcadores de actividad en la dentición en el grupo de Neandertales de la cueva de El Sidrón, grotte de l'Hortus y grotte de Spy, así como del microdesgaste dental en los fósiles de la cueva de El Sidrón y su comparación con los grupos de humanos modernos de cueva de La Paloma,

Indian Knoll, y otros especímenes procedentes de diversas fuentes bibliográficas. El esmalte dental es el material biológico más resistente que se conoce y una vez está formado, no se remodela, por lo que en él se puede "leer" la historia del diente y del individuo al que pertenece, tanto los eventos producidos durante su formación y desarrollo como mientras se encontraba en funcionamiento en el individuo, y tras la muerte de éste (Brothwell, 1981; Hillson, 1986, 1996; Kelley y Larsen, 1991; Dean, 1994; Scott y Turner, 1997). El estudio de la dentición de una especie extinta puede proporcionar información acerca de su desarrollo somático de su "life history" o historia vital, ya que el desarrollo dental está estrechamente ligado a al del individuo que posee esos dientes (Dean *et al*., 2001; Ramírez-Rozzi y Bermúdez de Castro, 2004; Smith *et al*., 2010, entre otros). También son indicadores de si el individuo sufrió algún episodio de estrés fisiológico durante su desarrollo (Ogilvie *et al*., 1989; Skinner, 1996; Cunha *et al*, 2004; Guatelli-Steinberg *et al*., 2004). Además, las diferencias morfológicas, de tamaño, en la expresión de alguna de las cúspides o crestas de la corona dental, se han utilizado para establecer relaciones filogenéticas, similitudes entre poblaciones o dar información acerca de las singularidades biológicas que definen a las poblaciones y especies (Wolpoff, 1979; Zilberman *et al*., 1992; Macho y Berner, 1993; Skinner, 1997; Stringer *et al*., 1997; Irish y Guatelli-Steinberg, 2003; Grine, 2004, 2005; Smith *et al*., 2005).

Por estas razones se ha escogido el estudio del desgaste dental, cálculo o sarro dental y estado de salud oral como aproximaciones al comportamiento de esta especie fósil.

A su vez, este gran objetivo se ha dividido en 4 sub-objetivos en función del tipo de marcador de actividad que se ha analizado. Así se han identificado los siguientes objetivos:

1. Identificación del número de individuos de la muestra de fósiles y caracterización paleobiológica de los Neandertales de El Sidrón, según diferentes metodologías (entre ellas, la asociación de piezas dentales aisladas gracias a la morfología y disposición de los surcos subverticales en las facetas interproximales de los dientes).

2. Estudio de la lateralidad manual en Neandertales mediante el estudio de la orientación de las estrías culturales. Análisis de la variabilidad de la lateralidad manual y de la asociación de las tareas para-masticatorias asociadas a este tipo de desgaste según la edad de los individuos, las implicaciones biológicas y cognitivas que pueden tener, y su comparación con *Homo sapiens*.

3. A raíz de la caracterización del desgaste dental asociado a otras actividades distintas de la propia masticación, se ha planteado el objetivo de estudiar si las sociedades Neandertales seguían el mismo patrón que las sociedades cazadoras-recolectoras actuales. Para averiguar el modo y grado en que los grupos Neandertales se estructuraban la realización de algunas tareas, se ha planteado el

estudio de la división del trabajo según la edad y el sexo en las actividades en las que se haya usado la dentición como adyuvante o "tercera mano" en numerosas tareas, como la preparación de pieles o el troceado de pedazos de carne que sujetaban con la boca. Se discuten las posibles implicaciones de esta división de las tareas en la vida de un grupo Neandertal.

4. El cuarto objetivo de esta tesis consiste en estudiar la diversidad trófica en grupos Neandertales y su relevancia ecológica, cómo se distribuyen los recursos energéticos entre los miembros adultos de grupos Neandertales aplicado al caso del grupo Neandertal de la Cueva de El Sidrón, y se ha comparando con *H. sapiens* de los yacimientos de cueva de la Paloma e Indian Knoll, en el contexto de otros individuos Neandertales y humanos actuales del Paleolítico superior procedentes de la literatura.

CAPÍTULO III - MUESTRAS Y MATERIALES DE ESTUDIO

La muestra principal de dientes estudiada en esta tesis corresponde a la colección de fósiles Neandertales encontrados en la Cueva de El Sidrón. Con el fin de contrastar los patrones encontrados en los Neandertales de El Sidrón, y poder obtener patrones de comportamiento más globales para la especie, también se han estudiado los fósiles de la Grotte de l'Hortus (Francia) y Grotte de Spy (Bélgica).

También se ha estudiado la dentición de *Homo sapiens* prehistóricos, del yacimiento de Cueva de la Paloma (Soto de la Regueras, Asturias) y el yacimiento de Indian Knoll (Green River, Kentucky, EEUU), y así poder comparar los patrones de comportamiento de estos grupos cazadores recolectores con los de los Neandertales, a quienes también se les atribuye un modo de vida cazador recolector.

III.1 Los Neandertales de la Cueva de El Sidrón (Asturias).

La Cueva de El Sidrón se encuentra en Asturias (Concejo de Piloña). Geológicamente, la cueva se encuentra situada en el Surco de Oviedo-Infiesto (Gervilla *et al*., 1978; Fortea *et al*., 2003) o Depresión Longitudinal (Martínez García, 1989; Fortea *et a*l., 2003), constituida por sedimentos mesozoicos y terciarios limitados al norte por relieves paleozoicos. Predominan los procesos de disolución y la entrada desde el exterior de materiales detríticos. En la

actualidad el proceso de karstificación sigue muy activo, situándose el nivel freático por debajo del nivel de la cueva (Fortea *et al*., 2003). El yacimiento propiamente dicho se encuentra en una galería lateral (Galería del Osario), en dirección E-O, transversal a la Galería Principal (dirección N-S). Los restos se encuentran en posición secundaria, cuyo depósito original puede estar localizado en una galería superior, y que por colapso de la misma, se desplazaron hasta su ubicación actual (Fortea *et al*., 2003; Cañaveras *et al*., 2011) .

En un principio, la colección estuvo dividida en dos submuestras. La primera estaba formada por 120 restos óseos neandertales que fueron recogidos sin control arqueológico (Egocheaga *et al*., 2000; Rosas y Aguirre, 1999; Fortea *et al*., 2003). La segunda formada por los restos que se han ido extrayendo desde el año 2000 mediante excavación sistemática (Fortea *et al*., 2003, 2008; Rosas *et al.*, 2006, 2012, 2013). Desde Enero de 2006 ambas submuestras se han reunido en una única colección que se encuentra depositada en el Museo Nacional de Ciencias Naturales (MNCN-CSIC, Madrid).

La colección de fósiles humanos de El Sidrón está formada por más de 2500 restos óseos y en la que están representadas todas las partes del esqueleto, constituyendo la mejor colección de fósiles neandertales de la Península Ibérica (Rosas *et al*., 2006, 2012, 2013). Recientes dataciones en hueso humano indican que la edad del conjunto fósil es de 48.400 ± 3200 años antes del presente (Wood *et al*., 2013).

El estado de conservación de los fósiles en el yacimiento es muy bueno y en algunos casos los restos se han conservado en conexión anatómica. Este excelente estado de conservación ha permitido el estudio de la histología

superficial del hueso en mandíbulas (Martínez-Maza *et al*., 2011) y en el hueso occipital (Kranioti *et al*., 2009), las petalias del cerebro (Bastir *et al*., 2008; Peña-Melián *et al*., 2011; Rosas *et al*., 2014), extracción y secuenciación de material genético (Krause *et al*., 2007; Lalueza-Fox *et al*., 2007; Fortea *et al*., 2008; Lalueza-Fox *et al*., 2008; Burbano *et al*., 2010; Green *et al*., 2010). Recientemente, el análisis del ADN mitocondrial ha permitido la caracterización de la sociedad neandertal como patrilocal, a la vez que confirmación genética del sexo de los individuos mediante la secuenciación del cromosoma "Y" (Lalueza-Fox *et al*., 2011).

La muestra dental correspondiente a este yacimiento y estudiada como pieza clave de esta tesis está formada por los 235 dientes recuperados en 1994 cuando se descubrió el yacimiento, y los recuperados durante las sucesivas excavaciones sistemáticas (años 2000 a 2014, incluido).

A continuación, se muestra una tabla con la muestra dental estudiada de este yacimiento.

SIGLA	DIENTE	SIGLA	DIENTE	SIGLA	DIENTE	SIGLA	DIENTE
SD-2400b	URC	SD-441	ULI2	SD-2020	URP3	SD-1863	ULM2
SD-2400c	URI2	SD-600	URP3	SD-322	LLI1	SD-1875	URI1
SD-2400d	URI1	SD-664	LLP4	SD-531	URM1	SD-1881	URI2
SD-2400e	ULI1	SDR-005a	LLM1	SD-768	dURm2	SD-599a	LRI1
SD-2400f	ULI2	SDR-005b	LLM2	SD-1220	ULC	SD-599b	LLI1
SD-2400g	ULC	SDR-005c	LLM3	SD-536b	URI2	SD-757	LLI2
SD-2400h	ULP3	SDR-006a	LLP3	SD-1327a	LRI2	SD-923	LRM3
SD-2400i	ULP4	SDR-006b	LLC	SD-1327b	LRI1	SD-925	LRP4
SD-2400j	ULM1	SDR-006c	LRI1	SD-1327c	LLI1	SD-933	LLP3
SD-2400k	ULM2	SDR-006d	LRI2	SD-1327d	LLI2	SD-934	LLP4

SIGLA	DIENTE	SIGLA	DIENTE	SIGLA	DIENTE	SIGLA	DIENTE
SD-2400l	ULM3	SDR-006e	LRC	SD-1327e	LLC	SD-935	LLC
SD-1105	URM1	SDR-006f	LRP3	SD-1327f	LLP3	SD-937	LRP3
SD-1510	LLM3	SDR-006g	LRP4	SD-1327g	LLP4	SD-1683a	URP4
SD-331a	URI1	SDR-006h	LRM1	SD-1327h	LLM1	SD-1683b	URM1
SD-331b	ULI1	SDR-006i	LRM2	SD-1327i	LLM2	SD-1882	LLM2
SD-370b	LRI2	SDR-141	URI2	SD-2010b	URM3	SD-209	LRC
SD-411	ULP4	SD-1240	URI2	SD-2010c	URM2	SD-331c	LLM1
SD-1019	LRI2	SD-1422	ULI1	SD-2010d	URM1	SD-355	LRI2
SD-1106	URP4	SD-1427b	ULM3	SD-2010e	URP4	SD-1707	URI2
SD-50	URP4	SD-1427c	ULM2	SD-2010f	URP3	SD-407	ULM1
SD-540	LLM2	SD-1427d	ULM1	SD-2010g	URC	SD-582	URI1
SD-551	URM2	SD-1427e	ULP4	SD-2010h	URI2	SD-639	ULP4
SD-566	URP3	SD-1427f	ULP3	SD-2010i	URI1	SD-657	LRM1
SD-621	URM3	SD-1427g	ULC	SD-2010j	ULI1	SD-920	LLM1
SD-741	ULM3	SD-1427h	ULI2	SD-2010k	ULI2	SD-921	LRI2
SD-756	LLM1	SD-1427i	URC	SD-2010l	ULC	SD-928	LLM2
SD-918	LRC	SD-1427j	URP3	SD-2010m	ULP3	SD-936	LRM3
SD-924	LRM3	SD-1427k	URP4	SD-1600b	dLLc	SD-1201	ULI1
SD-930	ULM2	SD-1427l	URM1	SD-1600c	dLLm1	SD-1202	ULC
SDR-012	ULM1	SD-1427m	URM2	SD-1600d	dLLm2	SD-299a	LLI2
SDR-013	URI2	SD-1427n	URM3	SD-1600e	LLM1	SD-312	ULP3
SDR-015	LRM1	SD-1439	URI1	SD-1600f	LLI2	SD-313	URI1
SD-1075	ULP3	SD-703	LRI1	SD-1600g	LLC	SD-2010n	ULP4
SD-1107	ULC	SDR-007a	LRI2	SD-1600h	LLP3	SD-2010o	ULM1
SD-1221	ULP4	SDR-007b	LLP3	SD-1600i	LLP4	SD-2010p	ULM2
SD-277	ULI1	SDR-007c	LLP4	SD-1600j	LLM2	SD-2010q	ULM3
SD-332	ULM3	SDR-007d	LLM1	SD-1660b	LRI1	SD-1161	ULC
SD-4	ULM2	SDR-007e	LLM2	SD-1660c	dLRc	SD-1574	LLI2
SD-500	LLP4	SDR-007f	LLM3	SD-1660d	dLRm1	SD-1575	LLP3
SD-501	LRP3	SDR-007g	LLINDET	SD-1660e	dLRm2	SD-1577	LLM1
SD-568	ULI2	SDR-007h	LLC	SD-1660f	LRM1	SD-1602	URM3
SD-61	LLC	SDR-014	LLI2	SD-1660g	LRI2	SD-1654	URP3

SIGLA	DIENTE	SIGLA	DIENTE	SIGLA	DIENTE	SIGLA	DIENTE
SD-772	UR3M	SD-1216a	LRM1	SD-1660h	LRC	SD-1789	URM2
SD-912	LLP3	SD-1216b	LRP3	SD-1660i	LRP3	SD-1833	URM1
SD-912b	LLINDET	SD-1216c	LRP4	SD-1660j	LRP4	SD-2007	ULM1
SD-1010	URC	SD-1217b	LRI1	SD-1660k	LRM2	SD-2040	URP4
SD-1054	URM1	SD-1217c	LLP3	SD-1716	dLRi2	SD-2158	ULM2
SD-1135	LRM3	SD-1217d	LLP4	SD-1719	ULI1	SD-303	LLP4
SD-1200a	ULP4	SD-1217e	LLM1	SD-1720	URC	SD-311	ULI1
SD-1200b	ULM1	SD-1218a	LLM2	SD-1721	dURc	SD-406	LLM3
SD-1200c	ULM2	SD-1218b	LLM3	SD-1824	URP4	SD-753	LLC
SD-1200d	ULM3	SD-1222	LRI2	SD-1862	ULM1	SD-926	LLI1
SD-221	URC	SD-2200b	URP3	SD-1576	ULP4	SD-1164	URM3
SD-278	LRI1	SD-2200c	URP4	SD-1603	ULM1	SD-1314	URM2
SD-763a	LRP4	SD-2200d	URM1	SD-1604	ULM2	SD-1572	ULI1
SD-913	ULC	SD-2200e	URM2	SD-1631	URM3	SD-1573	LLP3
SD-914	ULP3	SD-2200f	URM3	SD-1661	URC	SD-922	URM1
SD-915	ULP4	SD-1018	ULC	SD-1662	URP3	SD-927	LRP3
SD-916	ULM1	SD-780	LLM1	SD-755	LRM2		

Tabla III.1: Muestra dental estudiada correspondiente al yacimiento Neandertal de la Cueva de El Sidrón.

III.2 Los Neandertales de Grotte de l'Hortus (Francia).

La cueva de l'Hortus se encuentra en el sur de Fracia, a unos 20 Kms al norte de Montpellier, en la vertiente mediterránea. La cueva sirvió de refugio a los Neandertales durante la glaciación Würm, hace 30.000-60.000 años.

Se han identificado 20 individuos (de Lumley, 1973), y los fósiles se encuentran conservados en el European Center for Prehistoric Research in Tautavel (Francia). La edad de muerte de los individuos fue calculada en función del desarrollo y erupción dentaria (de Lumley, 1973). De los 20 individuos

identificados en el yacimiento, se han analizado 17 que son los que poseen dentición asociada.

SIGLA	DENTICIÓN	INDIVIDUO
HORTUS II y HORTUS III	Mandíbula y maxilar	Juvenil. Mismo individuo que Hortus III
HORTUS IV	Mandíbula incompleta	Adulto joven
HORTUS V	Mandíbula incompleta	Adulto joven
HORTUS VI	Mandíbula incompleta	Adulto joven
HORTUS VII	Maxilar incompleto	Adulto
HORTUS VIII y HORTUS XLVII	Maxilar incompleto	Adulto joven
HORTUS IX	Maxilar incompleto	Adulto joven
HORTUS X y HORTUS XLII	Maxilar incompleto	Adulto joven
HORTUS X bis	Maxilar incompleto	Adulto
HORTUS XI	Maxilar incompleto	Adulto maduro
HORTUS XII	Maxilar incompleto	Adulto maduro
HORTUS XII bis	Maxilar incompleto	Adulto maduro
HORTUS XIII	Maxilar incompleto	Adulto maduro
HORTUS XIII bis	Mandíbula incompleta	Adulto maduro
HORTUS XIV	Molar	Anciano
HORTUS XV	Maxilar incompleto	Infantil
HORTUS XVIII	Mandíbula incompleta	Adulto joven

Tabla III.2: Muestra dental analizada en esta tesis proveniente del yacimiento Grotte de l'Hortus.

III.3 Los Neandertales de Grotte de Spy (Bélgica).

Los fósiles de la cueva de Spy corresponden a dos individuos adultos y a un individuo infantil (del que sólo se ha recuperado dentición sin erupcionar). Los fósiles se encuentran en el Royal Institute of Natural Sciences en Bruselas, Bélgica. Se ha datado el yacimiento en aproximadamente hace 36.000 años (Semal *et al*., 2009, 2011). Se han seleccionado para el estudio los individuos adultos Spy I y Spy II. Según Schwartz y Tattersall (2002), ambos individuos pueden ser masculinos según su anatomía, pero según el volumen endocraneal, Spy II podría ser un individuo femenino (Holloway *et al*., 2005). Recientemente Chapman *et al*. (2013) han reconstruido el esqueleto de Spy II, indicando que se trata, efectivamente, de un individuo de sexo masculino. Actualmente se está llevando a cabo una reasignación del sexo de los individuos (P. Semal, comunicación personal).

Espécimen	Sexo	Edad	Dentición
SPY I	Masculino	Adulto	ULI2; URI1; URC; LLI2
SPY II	Masculino	Adulto	ULC; ULI1; URC; LLC; LLI1; LRI2

Tabla III.3: Muestra dental analizada en esta tesis proveniente del yacimiento Grotte de Spy.

III.4 Cazadores recolectores del Paleolítico superior de la Cueva de la Paloma (Asturias).

El yacimiento fue excavado entre 1914 y 1915 por el Dr. Eduardo Hernández Pacheco (Hernández-Pacheco, 1923; Hoyos *et al*., 1980). Se han identificado de 9 niveles arqueológicos, de los cuales sólo 3 contienen restos humanos: nivel 9 asociado a la cultura Magdaleniense inferior, el nivel 8 asociado a la cultura Magdaleniense, y el nivel 2 asociado a la cultura Aziliense (Hernández-Pacheco, 1923; Barandiarán, 1971; Hoyos *et al*., 1980; Straus, 1992; Meiklejohn, 2009). Los restos humanos se encuentran catalogados en la colección de Paleontología y Prehistoria del Museo Nacional de Ciencias Naturales (MNCN-CSIC), y esta es la primera vez que están siendo estudiados.

Para esta tesis, se han considerado los restos humanos pertenecientes a individuos adultos [M3 en oclusión, Alqahtani *et al*., (2010)] de los niveles Magdalenienses. El esmalte dental de los molares se conserva sin alteraciones de origen tafonómico, y no presentan un elevado grado de desgaste oclusal. El sexo se ha estimado en las mandíbulas (siguiendo a Rosas *et al*., 2002).

SIGLA	SEXO Y EDAD	DENTICIÓN
MNCN 1363-1367-1371-6614-6563	Femenino	LLM1, LLM2
MNCN 1364-1365	Femenino	LLM1, LLM2, LRM2
MNCN 1366-1370	Masculino	LLM2

Tabla III.4: Muestra dental analizada en esta tesis proveniente del yacimiento Cueva de la Paloma

III.5 Cazadores recolectores de Indian Knoll (Kentucky, EEUU).

La colección de restos óseos conocida como Indian Knoll pertenece a una población prehistórica que ocupaba el territorio del río Green en el estado de Kentucky (EEUU). El yacimiento se adscribe al periodo Arcaico tardío y medio (5590–4530 años AC; Morey *et al*., 2002), y fue excavado en 1915 y se terminó de excavar en los años 30 y 40 del siglo pasado (Webb, 1974).

Los indios que ocuparon esa zona eran cazadores recolectores y su dieta estaba basada principalmente en carne de ciervo, pero también cazaban pequeños pájaros y pavo. Vivieron en una ensenada (Morey y Crothers, 1998; Morey *et al*., 2002), por lo que los mejillones eran muy abundantes en la zona y formaron una parte importante de su dieta, al menos estacionalmente (Webb, 1974).

Parte de los restos esqueléticos se encuentran depositados en el departamento de Antropología en el National Museum of Natural History (Smithsonian Institution, Washington D.C.). La muestra que se ha estudiado consiste en 65 individuos, cuya dentición mandibular y maxilar está prácticamente completa. Los perfiles demográficos de los individuos se han obtenido de diversos estudios previos (Snow *et al*., 1948; Webb, 1974).

Sigla	Individuo	Edad	Sexo
P290015-0	BURIAL 226	Adulto	Masculino
P290016-0	BURIAL 231	Adolescente	Masculino
P290017-0	BURIAL 119	Adulto	Masculino
P290018-0	BURIAL 166	Adulto	Masculino
P290021-0	BURIAL 24	Adulto	Masculino
P290025-0	BURIAL 243, NO. 3	Adulto	Masculino
P290026-0	BURIAL 268	Adulto	Masculino

Sigla	Individuo	Edad	Sexo
P290044-0	BURIAL 179	Adolescente	Femenino
P290030-0	BURIAL 233	Adulto	Masculino
P290046-0	BURIAL 76	Adolescente	Femenino
P290048-0	BURIAL 138	Adulto	Femenino
P290049-0	BURIAL 176	Juvenil	Femenino
P290051-0	BURIAL 14	Adulto	Femenino
P290035-0	BURIAL 255	Adulto	Masculino
P290053-0	BURIAL 142	Adulto	Femenino
P290037-0	BURIAL 53	Adulto	Masculino
P290055-0	BURIAL 245	Adulto	Masculino
P290038-0	BURIAL 210	Adulto	Masculino
P290058-0	BURIAL 259	Adulto	Femenino
P290065-0	BURIAL 72	Adolescente	Femenino
P290050-0	BURIAL 44	Adulto	Femenino
P290039-0	BURIAL 278	Adulto	Masculino
P290040-0	BURIAL 152	Adulto	Masculino
P290041-0	BURIAL 202	Adulto	Masculino
P290063-0	BURIAL 292	Adulto	Femenino
P290064-0	BURIAL 132	Adulto	Femenino
P290068-0	BURIAL 258	Adulto	Femenino
P290042-0	BURIAL 61	Adulto	Masculino
P290043-0	BURIAL 57	Adulto	Masculino
P290071-0	BURIAL 118	Adulto	Femenino
P290072-0	BURIAL 249	Adulto	Femenino
P290045-0	BURIAL 52	Adulto	Masculino
P290076-0	BURIAL 235	Juvenil	Indeterminado
P290077-0	BURIAL 264	Adulto	Femenino
P290078-0	BURIAL 229	Juvenil	Femenino
P290079-0	BURIAL 257	Juvenil	Indeterminado
P290080-0	BURIAL 199	Adulto	Femenino
P290081-0	BURIAL 236	Juvenil	Indeterminado
P290082-0	BURIAL 2	Adulto	Masculino
P290047-0	BURIAL 205	Adulto	Masculino
P290052-0	BURIAL 95	Adulto	Masculino
P290054-0	BURIAL 89	Adulto	Masculino
P290060-0	BURIAL 260	Adulto	Femenino
P290000-0	BURIAL 3	Adulto	Femenino
P290006-0	BURIAL 192	Adulto	Femenino
P290007-0	BURIAL 11	Adulto	Femenino
P290057-0	BURIAL 110	Adulto	Masculino

Sigla	Individuo	Edad	Sexo
P290059-0	BURIAL 47	Adulto	Masculino
P290061-0	BURIAL 169	Adulto	Masculino
P290019-0	BURIAL 161	Adulto	Femenino
P290020-0	BURIAL 4	Adulto	Masculino
P290062-0	BURIAL 187	Adulto	Masculino
P290022-0	-	Adulto	Femenino
P290023-0	BURIAL 183	Adulto	Masculino
P290024-0	BURIAL 188	Adulto	Femenino
P290069-0	BURIAL 50	Adulto	Masculino
P290027-0	BURIAL 113	Adolescente	Femenino
P290028-0	BURIAL 148	Adulto	Femenino
P290029-0	BURIAL 111	Adulto	Indeterminado
P290070-0	BURIAL 74	Adulto	Masculino
P290032-0	BURIAL 131	Adulto	Femenino
P290033-0	BURIAL 239	Adulto	Femenino
P290034-0	BURIAL 294	Adulto	Femenino
P290073-0	BURIAL 85	Adulto	Masculino
P290036-0	BURIAL 184	Adulto	Masculino

Tabla III.5: Muestra dental analizada en esta tesis proveniente del yacimiento Indian Knoll.

CAPÍTULO IV - IDENTIFICACIÓN DEL NÚMERO DE INDIVIDUOS EN MUESTRAS DE FÓSILES

Los resultados de estos estudios han sido publicados en:

Rosas, A., Estalrrich, A., García-Vargas, S., García-Tabernero, A., Huguet, R., Lalueza-Fox, C., de la Rasilla, M., 2013. Identification of Neandertal individuals in fragmentary fossil assemblages by means of tooth associations: The case of El Sidrón (Asturias, Spain). Comptes Rendus Palevol, 12(5): 279-291.

Estalrrich, A., Rosas, A., García-Vargas, S., García-Tabernero, A., Santamaría, D., de la Rasilla, M., 2011. Brief Communication. Subvertical grooves on interproximal wear facets from the El Sidrón Neandertal dental sample. American Journal of Physical Anthropology, 144: 145–161.

En un yacimiento en el que los fósiles aparecen fragmentados, es esencial la identificación del número mínimo de individuos en él representados (Casteel, 1977; Horton, 1984), y la precisión con que esta identificación sea hecha, es determinante para todos los estudios que se hagan a partir de esta estimación (Rosas *et al*., 2013).

En el yacimiento de la Cueva de El Sidrón, el material esquelético más abundante es la dentición. Y es a partir de este resto que se ha estimado el NMI de la muestra. Además, los dientes permiten obtener otro tipo de información también muy útil para la identificación de los individuos como la edad, estado de salud (presencia de sarro, paleopatologías, hipoplasias durante su crecimiento, etc).

IV.1 Breve descripción de la metodología

Para establecer el NMI, primero se ha identificado la pieza dental más representada.

A continuación, se han definido 12 criterios de asociación de los dientes aislados, con el fin de poder caracterizar a los individuos identificados previamente:

1._ Los dientes que han aparecido en conexión anatómica (exista o no un soporte óseo que los una), pertenecen al mismo individuo.

2._ El diente encaja exactamente en el alveolo correspondiente de la mandíbula o del maxilar.

3._ Las facetas interproximales coinciden con las de su diente adyacente, y además de considerar el tamaño y forma de la faceta, se ha considerado el patrón de distribución de los surcos subverticales, que en esta muestra se han caracterizado ya previamente (Estalrrich *et al*., 2011). La metodología de análisis de este criterio se explica en un apartado específico. La similitud de 2 facetas (imágenes especulares) indica que los dientes conectan y van asociados.

4._ El grado de desgaste oclusal debe ser coherente. Se ha trabajado con la escala de propuesta por Skinner (1997).

5._ Coherencia en el estado de desarrollo, calcificación y erupción dentaria (AlQahtani *et al*., 2010).

6._ Similitud en la morfología de la corona y de la raíz a la hora de identificar antímeros. Se han medido los diámetros mesiodistal y bucolingual, comparado el tamaño y localización de las cúspides y crestas, y otras características morfológicas siguiendo los estándares del sistema ASUDAS (Turner II *et al.*,1991).

Estos 6 primeros criterios son lo que más robustez proporcionan a las asociaciones dentales. Los siguientes 6 criterios, aunque menos robustos y generales, han permitido realizar asociaciones en casos particulares, dado que las características que los siguientes criterios definen están más relacionadas con cualidades propias de cada individuo.

7._ Presencia de hipoplasia del esmalte.

8._ Presencia, abundancia y localización de cálculo dental o sarro.

9._ Patologías (Prieto, 2005; Dean *et al*., 2013).

10._ Mellas del esmalte dental

11._ Abundancia de estrías culturales en la cara labial de la dentición anterior.

12._ Factores tafonómicos: color, similitud de las concreciones calcáreas, etc.

Cada uno de los rasgos de desgaste dental considerados en este asociación, ha sido examinado mediante lupa binocular (Leica SD6©), microscopio óptico (Olympus©BX51) y microscopio electrónico de barrido, ESEM (Fei Quanta 200©).

IV.2 Resultados

La pieza dental más representada en el yacimiento es el primer molar mandibular izquierdo (LLM1), del que se han recuperado 10 ejemplares. 5 LLM1 han aparecido en conexión anatómica, es decir, se encontraban en sus respectivas mandíbulas (Adulto 1, Adulto 2, Adulto 3, Adulto 5, Juvenil 1). A partir de los otros 5 LLM1 aislados, se han hecho las correspondientes asociaciones (Adulto 4, Adulto 6, Adulto 7, Adolescente 1, Adolescente 2). Durante este proceso de asociación, se ha identificado un nuevo individuo (Adolescente 3), dado que la asociación dental realizada con corresponde a ninguno de los individuos anteriores (bien por edad, o por repetición de piezas dentales).

Además de la identificación de los individuos mediante la dentición, diversos elementos postcraneales han permitido identificar a dos individuos más: un infantil de 1,5-3 años de edad (Egocheaga y Sierra, 2005; Rosas *et al*., 2006), y otro individuo juvenil.

Así pues, el yacimiento Neandertal de la cueva de El Sidrón está compuesto por un número mínimo de 13 individuos: 3 adultos masculinos, 3

adultos femeninos, 1 adulto sin sexo identificado, 2 adolescentes masculinos, 1 adolescente posiblemente femenino, 1 juvenil masculino, 1 juvenil sin sexo identificado y e individuo infantil sin sexo identificado.

IV.3 Caracterización de los surcos subverticales

Los surcos subverticales (*subvertical grooves*, en inglés) son grandes canales que se pueden observar a simple vista en las facetas mesial y distal de contacto interdental en algunas poblaciones humanas. Aparecen con mayor frecuencia en los molares que en los premolares. Tienen una dirección oclusocervical, de forma, generalmente, más o menos radial, y rara vez son paralelas. Suelen aparecer en número variable, desde 1 hasta 10 (Kaidonis *et al*. 1992; Villa y Giacobini, 1995; Pérez-Pérez *et al*., 2003; Egocheaga *et al*., 2004).

Estos surcos se han observado en los Homínidos fósiles Atapuerca-Sima de los Huesos (Pérez-Pérez *et al*., 2003), *Homo neanderthalensis* de los yacimientos de Figueira Brava en Portugal (Antunes y Cunha, 1992; Egocheaga *et al*., 2004), Caverna delle Fate en Italia (Giacobini *et al*., 1984), Grotte du Rochelot (Poisson et al., 2002) y El Sidrón (Egocheaga *et al*., 2004; Estarrich *et al*., 2011), y *Homo sapiens* de Qafzeh en Israel (Vandermeersch, 1981). También se ha observado que los surcos son más frecuentes entre los Aborígenes Australianos, que entre la población australiana no Aborigen (Kaidonis *et al.*, 1992).

Respecto al origen de estos surcos existen diversas propuestas, y el tema aún está siendo investigado. Algunos autores proponen que su formación se debe a procesos de abrasión dental producidos durante la vida del individuo por el

consumo de alimentos duros y elevado estrés masticatorio (Wolpoff, 1971) o a sustancias ácidas en la dieta que se introducen en el espacio interdental durante la masticación, unido a las fuerzas que se producen durante este proceso (Villa y Giacobini, 1995). La mayor frecuencia de la presencia de estas formaciones en los Neandertales se podría deber a la asociación de una dieta dura, mayor fuerza masticatoria y a la morfología y estructura de la corona del diente características de estas poblaciones (Pérez-Pérez *et al*., 2003).

Los surcos subverticales se pueden apreciar a simple vista en las facetas interproximales Pero para verificar la morfología se ha utilizado una lupa binocular (Leica S6D®) de hasta 40x, equipada con un cámara fotográfica digital y un microscopio electrónico de barrido con cámara ambiental (Fei Quanta 2001 ESEM, de las siglas de *Environmental Scanning Electron Microscope*) para obtener más detalle sobre su morfología y la de la faceta.

Los dientes se han observado directamente en el microscopio. En algunos casos, debido a que algunos dientes se encuentran en sus respectivas mandíbulas y maxilares, ha sido necesario preparar réplicas de alta resolución. Para ello, primero se han limpiado los dientes con acetona y agua destilada y un pincel de pelo de marta. Cuando se han secado, se ha realizado el molde o negativo con un material de impresión hidrofílico de vinil polisiloxano (con el nombre comercial de Exaflex ®) de baja viscosidad. Este material ha dado muy buenos resultados a la hora de replicar fósiles (Bromage, 1987; Martínez-Maza *et al*., 2002, 2006, 2011; Kranioti *et al*., 2009). La réplica o positivo se ha realizado con resina de poliuretano (marca comercial Feropur ®), que tiene buena capacidad de resolución y un tiempo de fraguado muy rápido. A continuación, la réplicas se

han metalizado con una fina capa de oro (Sputter Coater EMYTECH®) para permitir la observación en el microscopio electrónico, ya que los electrones deben rebotar en la superficie del molde para poder obtener una imagen del mismo, y las resinas empleadas en la reproducción de fósiles absorben los electrones, con lo cual no se obtiene ninguna imagen.

Con el programa Image J (Rasband, 2006) se ha medido la longitud de los surcos, su anchura y en algunos casos, la profundidad del surco en el punto medio en las imágenes obtenidas en el ESEM.

Con el objetivo de conocer cual es la relación entre el número de surcos subverticales en una faceta interproximal (variable dependiente o variable de respuesta) y un conjunto de variables independientes o explicativas (el grado de desgaste oclusal; la anchura de la faceta; su posición en el diente, es decir mesial o distal; y la edad estimada del individuo al que el diente pertenece), se ha realizado un análisis estadístico mediante Modelos Lineales Generalizados (GLM, del inglés *General Linear Models*).

Así, se ha obtenido que 60 de los 93 dientes analizados (64.5%) tienen al menos un surco subvertical en la faceta interproximal. Se han contabilizado un total de 85 facetas interproximales con surcos subverticales. El 50% de la dentición anterior presentan surcos subverticales. Hasta este momento, nunca se habían descrito estos sucos en las facetas interproximales de caninos e incisivos. El 76.5% de los premolares y molares de la muestra presenta surcos subverticales.

El número de surcos por faceta varía de 1 a 4 en las facetas de la dentición anterior y de 1 a 8 en las de la dentición posterior, siendo las facetas distales de los P4 y las mesiales y distales de los M1 las que más surcos presentan.

Los resultados del análisis GLM indica que la única variable explicativa respecto al número de surcos es la anchura de la faceta interproximal. Ni el grado de desgaste oclusal, ni su posición mesial o distal en el diente, ni la edad del individuo al que están asociados, muestran ninguna diferencia estadísticamente significativa. Es más, los surcos más profundos se han encontrado en los dientes que tienen un menor grado de desgaste oclusal [Grados 2 y 3 de la escala propuesta por Skinner (1997)], mientras que los más someros aparecen en dientes con un grado de desgaste oclusal medio [Grados 4 y 5 3 de la escala propuesta por Skinner (1997)].

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Identification of Neandertal individuals in fragmentary fossil assemblages by means of tooth associations: The case of El Sidrón (Asturias, Spain)

Identification d'individus néandertaliens dans des assemblages fossiles fragmentaires au moyen des associations dentaires : le cas d'El Sidrón (Asturies, Espagne)

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ABSTRACT

Identification of the individuals represented in a fragmentary fossil assemblage is a key step in paleobiological research, as ensuing organism-level studies, as well as sampling strategies (e.g., DNA, isotopes, dating, etc.), may depend on the reliability of such estimates. In the human fossil record, dental remains represent the most abundant and informative material, allowing individual identification on the basis of a variety of diagnostic criteria. In this paper, we present a procedure for sequential association of the dental remains and the identification of the minimum number of individuals (MNI) represented in the 49,000-year-old Neandertal assemblage from El Sidrón (Asturias, Spain). In order to quantify the possible association errors, the 12 criteria used in this study are organised according to three levels of reliability. Following this procedure, a minimum of 13 individuals (seven adults, three adolescents, two juveniles and one infant) have been identified at El Sidrón, two of them uniquely represented by postcranial elements. A next step in this investigation foresees the development of methods for associating postcranial elements with the dentally-based identified individuals.

Mots clés :
El Sidrón
Néandertaliens

RÉSUMÉ

L'identification du nombre d'individus représentés dans un assemblage fossile fragmentaire est une étape clé dans les recherches paléobiologiques, étant donné que les études postérieures à l'échelle de l'organisme, mais aussi les stratégies d'échantillonnage

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Associations dentaires
Paléolithique moyen
Espagne

(ex., ADN, isotopes, datations, etc.) peuvent dépendre de la fiabilité de ces estimations. Dans le registre humain fossile, les restes dentaires représentent le matériel le plus abondant et informatif pour l'identification des individus sur la base d'une variété de critères diagnostiques. Dans cet article, nous présentons une procédure pour l'association séquentielle d'éléments dentaires et l'identification du nombre minimal d'individus (MNI) représentés dans l'assemblage des restes néandertaliens d'El Sidrón (Asturies, Espagne), daté de 49 000 ans. Pour sécuriser les associations dentaires et identifier les erreurs possibles, les 12 critères utilisés dans cette étude ont été répartis selon trois niveaux de fiabilité. D'après cette procédure analytique, un nombre minimal de 13 individus (sept adultes, trois adolescents, deux juvéniles et un enfant) a été identifié à El Sidrón, deux d'entre eux étant uniquement représentés par des éléments postcrâniens. Une étape succédant à cette phase analytique prévoit le développement des méthodes pour l'attribution d'éléments postcrâniens à des individus identifiés uniquement par des associations dentaires.

1. Introduction

Among the currently active Middle Paleolithic excavation projects, the El Sidrón site (Asturias, Spain) has a significant place in Neandertal paleobiological studies. A number of exceptional conditions make El Sidrón a singular site. The fossil assemblage is concentrated in a small cave deposit and is composed of a large number of human skeletal remains belonging to several individuals (Rosas et al., 2006, 2012) with familial relationships (Lalueza-Fox et al., 2011). There is a limited presence of faunal remains and a relative abundance of refitting stone tools (Santamaría et al., 2010). In addition, evidence of cannibalism has been demonstrated in this sample (Rosas et al., 2006). At present, over 2300 specimens have been recovered (Fortea et al., 2003; Rosas et al., 2006, 2012). Cutting edge techniques are applied for the investigation of this assemblage, including ancient DNA sampling in the field (Fortea et al., 2008) and laboratory analyses (Lalueza-Fox et al., 2006, 2007, 2008, 2011), ultrafiltration radiocarbon datings (Torres et al., 2010; Wood et al., 2013), molecular dental calculus (Hardy et al., 2012) and morphometric analyses (Bastir et al., 2010; Rosas et al., 2008).

Fossil skeletal elements frequently appear disarticulated in the archaeo-paleontological record, even in those cases where the remains come from the same body (Haglund and Sorg, 1997; Lyman, 1994; Ubelaker, 1989; White and Folkens, 2005). Diverse sedimentary and taphonomical factors contribute to skeletal disarticulation and the scattering of the remains (Lyman, 1994). The re-assembling of the original anatomical units and the association of different fossil specimens to a single individual is a key step in taphonomical and paleobiological studies (Trinkaus et al., 2000). The El Sidrón Neandertal sample represents a good example of this widespread problem.

Several possibilities for understanding diverse cultural, taphonomic and evolutionary aspects arise when these topics are approached at organismic level. A large spectrum of analyses demands a particular strategy for sampling, which in turn requires the individual affiliation of an isolated specimen (e.g., a tooth) to be ascertained. For instance, a precise assessment of the number of individuals represented in a fossil hominin sample can yield new valuable information regarding the social structure of the group and the site function, also allowing for significant time saving when analysing individual mtDNA. Many other examples can be mentioned, such as nuclear DNA and isotopic analyses, dating, etc. Likewise, a prior characterization of the identity and biological attributes of the individuals represented in a fossil sample is required for paleodemographic studies (Bermúdez de Castro et al., 2004, 2006; Trinkaus, 1995).

Teeth are the most represented elements in the paleoanthropological record (Hillson, 1986), both because of their relative abundance within the organism and relative hardness and durability. They also preserve extremely valuable information about phylogenetic history (morphology, e.g., Bailey and Lynch, 2005; Moggi-Cecchi et al., 2006), life-history (developmental patterns, e.g., Macchiarelli et al., 2006; Smith et al., 2007), paleobiology (diet, use of the mouth, etc., e.g., Grine et al., 2006; Molnar, 1972), and individual life events (physiological stresses, e.g., Guatelli-Steinberg, 2009; Ogilvie et al., 1989). As a whole, these characteristics grant to the dentition a high degree of individual specificity. Accordingly, tooth associations are an essential component of paleobiological analyses of fossil assemblages because subsequent studies will rely upon the accuracy of these individual reconstructions (Aguirre et al., 1986; Gençturk et al., 2008; Moggi-Cecchi et al., 2006). However, the interpretation of tooth associations are largely based on the experience of the researcher (e.g., Aguirre et al., 1986; Bermúdez de Castro et al., 2004, 2006; Gençturk et al., 2008; Moggi-Cecchi et al., 2006; Wolpoff, 1979).

Given that any progress in the characterization of the paleobiological profile of the Neandertals from El Sidrón will greatly benefit from a reliable assessment of tooth associations and related number of individuals, in this study we present the procedures followed for assembling the isolated teeth.

2. Material and methods

2.1. Material

2.1.1. The site

The karstic cave of El Sidrón, with a total length of 3700 m, is situated in the "Surco Oviedo-Infiesto", a band of Mesozoic and Cenozoic sediments limited to the north and south by Paleozoic reliefs. The main gallery of the cave,

called "Galería del Río", has lateral ramifications located at intervals of 50–100 m running NE-SW to north-south. All the findings come from a restricted lateral gallery inside the cave, "Galería del Osario", which is oriented north-south. Sediments are mostly sands and clays, with gravel layers indicating variations in hydraulic energy (Fortea et al., 2003; Santamaría et al., 2010).

In 1994, an exceptional set of human fossils was accidentally found and gave rise to the methodical excavation and multidisciplinary study of the site (Fortea et al., 2003). As a result, a significant archaeo-paleontological record, for the most part composed of Neandertal remains, has being recovered since 2000 (Rosas and Aguirre, 1999; Rosas et al., 2006). At present, more than 2300 human remains have been retrieved, representing several individuals whose remains are actually found commingled. All the skeletal parts are represented and some of the remains are in anatomical connection. There is also a moderate occurrence of Middle Paleolithic stone tools ($n = 415$), and very few faunal remains. Refitting of bone fragments and of 67 lithic artefacts proves unequivocally a single archaeological deposit (Santamaría et al., 2010).

The El Sidrón remains preserve ancient DNA, both mtDNA (Lalueza-Fox et al., 2005, 2006, 2011) and nuclear DNA (Krause et al., 2007; Lalueza-Fox et al., 2007, 2008). In order to avoid bone contamination with modern human DNA, and also to preserve DNA integrity by means of freezing the selected samples, a specific excavation protocol was implemented at the site (Fortea et al., 2008).

The detailed taphonomy of the site is currently under study but the following scenario can already be suggested: the remains are in a secondary position; the original deposition place occurred elsewhere (Fortea et al., 2003); and the assemblage arrived at its present location after the collapse of an upper gallery close to the "Galería del Osario" (Cañaveras et al., 2011; Sánchez-Moral et al., 2007). A multi-dating approach has been undertaken at the site, giving a consistent date of ~49,000 years for the Neandertal fossil assemblage (Torres et al., 2010; Wood et al., 2013).

2.1.2. The fossil dental sample

Coming into the 2012 field season, the El Sidrón dental sample was composed of 222 teeth. There are 108 lower teeth (61 from the left, 47 from the right side), of which 58 are enclosed in their alveoli (*in situ*) and 50 are isolated. The upper dentition is represented by 114 teeth (55 left, 59 right), of which 44 are *in situ* and 70 are isolated. There is one dental set in anatomical contact (SD-1327a to SD-1327i) though the bony support (mandible) no longer exists. Two nearly complete mandibles, two hemi mandibles and two more small mandibular fragments are preserved. In addition, two complete maxilla (which include 29 teeth in their alveoli) and three fragments of maxillae (two with four teeth each and one more with five teeth) are also preserved (Tables 1 and 2).

2.2. Methods

The study was carried out in three steps. First, the identification of the minimum number of individuals (MNI) and tooth row associations in the lower dentition. Second, the same procedure was independently followed for the upper dentition. Finally, the matching of the lower and the upper dental assemblages was considered. The number of mandibular teeth found *in situ* ($n = 58$) exceeding that of the maxillary ones ($n = 44$) was decisive in starting the analysis with the lower dentition.

The MNI was primarily established by the identification of the most common tooth. Nonetheless, other elements indicating biological age incompatible with that established from the dental remains can be used to define new individuals. For instance, the presence of postcranial elements from immature individuals not represented by dental specimens may lead to the identification of new individuals.

Individuals were assigned to one of the following five age categories adapted from Bogin (1988, 1997, 2009; see also Bogin and Smith, 1996):

- "infant" (ending at the completion of the eruption of the deciduous dentition);
- "childhood" (when the deciduous dentition is fully in occlusion);
- "juvenile" (from the time in which the first permanent molar is erupted to the loss of the second deciduous molar);
- "adolescent" (third molar eruption);
- and "adult" (the third molar is in occlusion with different degrees of wear).

Age at death for the non-adult individuals is primarily based on dental formation chronology proposed by AlQahtani et al. (2010). Among the adults, two categories have been distinguished, young and mature, based on differences in the degree of occlusal dental wear assessed following Skinner (1997). Regarding post-cranial immature remains, age at death was estimated following the epiphyseal fusion times (Scheuer and Black, 2000). The sex of the individuals was estimated using measurements of the mandibular corpus and intra-sample relative differences in canine tooth size (following Bermúdez de Castro et al., 2001, 2006; Rosas et al., 2002).

2.2.1. Order of tooth row association

For tooth row association assessment, we systematically followed the procedure summarised in Fig. 1. Starting from the most represented tooth in the sample, the reference tooth, we looked for its conjoining distal tooth (proceeding in a distal direction due to the sample composition). Once this element was identified, we looked for the antimere of the reference tooth. In searching for the antimere, we looked for a quasi identically sized and shaped specimen, as well as for its congruence in terms of wear at the available corresponding tooth class sub-sample. The next step was establishing the distal conjoining of the antimere after which we examined the reference tooth row looking for the next conjoining element. This process was reiterated.

Table 1
Complete list of dental specimens from El Sidrón (Asturias, Spain) assigned to the individuals identified so far in the sample. Assignation follows three levels of reliability (see text for details).
Tableau 1
Liste complète des spécimens dentaires d'El Sidrón (Asturies, Espagne) assignés à chacun des individus de l'échantillon identifiés à ce jour. L'attribution suit trois niveaux de fiabilité (voir les détails dans le texte).

	Level 1	Level 2	Level 3
Individual	Anatomical connection Fitting into the socket Interproximal wear facets and subvertical grooves Occlusal wear degree Developmental age Morphology Enamel hypoplasia Dental calculus Other pathologies Para-masticatory dental wear Taphonomical features	Interproximal wear facets Occlusal wear degree Developmental age Morphology Enamel hypoplasia Dental calculus Para-masticatory dental wear Taphonomical features	Occlusal wear degree Developmental age Morphology
Adult 1			
Upper dentition	SD-1200a; $\underline{LP^4}$ SD-1200b; $\underline{LM^1}$ SD-1200c; $\underline{LM^2}$ SD-1200d; $\underline{LM^3}$ SD-312; LP^3 SD-1202; LC SD-441; LI^2 SD-1201; LI^1 SD-313; RI^1	SD-1054; RM^1 SDR-141; RI^2 SD-1010; RC SD-600; RP^3	
Lower dentition	SDR-005a; $\underline{LM_1}$ SDR-005b; $\underline{LM_2}$ SDR-005c; $\underline{LM_3}$ SDR-006a; $\underline{LP_3}$ SDR-006b; $\underline{LC}$ SDR-006c; $\underline{RI_1}$ SDR-006d; $\underline{RI_2}$ SDR-006e; $\underline{RC}$ SDR-006f; $\underline{RP_3}$ SDR-006 g; $\underline{RP_4}$ SDR-006 h; $\underline{RM_1}$ SDR-006i; $\underline{RM_2}$ SD-1135; RM_3 SD-664; LP_4	SD-299a; LI_2	
Adult 2			
Upper dentition	SD-1427b; $\underline{LM^3}$ SD-1427c; $\underline{LM^2}$ SD-1427d; $\underline{LM^1}$ SD-1427e; $\underline{LP^4}$ SD-1427f; $\underline{LP^3}$ SD-1427 g; $\underline{LC}$ SD-1427 h; $\underline{LI^2}$ SD-1427i; $\underline{RC}$ SD-1427j; $\underline{RP^3}$ SD-1427k; $\underline{RP^4}$ SD-1427l; $\underline{RM^1}$ SD-1427 m; $\underline{RM^2}$ SD-1427n; $\underline{RM^3}$	SD-1240; RI^2 SD-1439; LI^1 SD-1422; RI^1	
Lower dentition	SDR-007a; $\underline{RI_2}$ SDR-007b; $\underline{LP_3}$ SDR-007c; $\underline{LP_4}$ SDR-007d; $\underline{LM_1}$ SDR-007e; $\underline{LM_2}$ SDR-007f; $\underline{LM_3}$ SDR-007 g; C anomalous SDR-007 h; C impacted	SDR-014: LI_2 SD-703; RI_1	
Adult 3			
Upper dentition	SD-2200b; $\underline{RP^3}$ SD-2200c; $\underline{RP^4}$ SD-2200d; $\underline{RM^1}$ SD-2200e; $\underline{RM^2}$ SD-2200f; $\underline{RM^3}$		SD-1220; LC

Table 1 (*Continued*)

	Level 1	Level 2	Level 3
Lower dentition	SD-1218b; LM_3		**SD-1222; RI_2**
	SD-1218a; LM_2		**SD-1217b: RI_1**
	SD-1217c; LP_3		
	SD-1217d; LP_4		
	SD-1217e; LM_1		
	SD-1216a; RP_3		
	SD-1216b; RP_4		
	SD-1216c; RM_1		
Adult 4			
Upper dentition	SD-1603; LM^1	SD-1018; LC	SD-1572; LI^1
	SD-1604; LM^2	SD-1661; RC	SD-1576; LP^4
	SD-1683a; RP^4	SD-1314; RM^2	
	SD-1683b; RM^1	SD-1662; RP^3	
		SD-1631; RM^3	
Lower dentition	SD-331c; LM_1	SD-209; RC	SD-923; RM_3
	SD-934; LP_4	SD-933; LP_3	**SD-757; LI_2**
		SD-935; LC	**SD-599b; LI_1**
		SD-937; RP_3	**SD-599a; RI_1**
		SD-925; RP_4	**SD-355; RI_2**
		SD-1882; LM_2	
Adult 5			
Upper dentition	SD-2010b; LM^3		
	SD-2010c; LM^2		
	SD-2010d; LM^1		
	SD-2010e; LP^4		
	SD-2010f; LP^3		
	SD-2010 g; LC		
	SD-2010 h; LI^2		
	SD-2010i; LI^1		
	SD-2010j; RI^1		
	SD-2010k; RI^2		
	SD-2010l; RC		
	SD-2010 m; RP^3		
	SD-2010n; RP^4		
	SD-2010o; RM^1		
	SD-2010p; RM^2		
	SD-2010q; RM^3		
Lower dentition	SD-1327a; RI_2		
	SD-1327b; RI_1		
	SD-1327c; LI_1		
	SD-1327d; LI_2		
	SD-1327e; LC		
	SD-1327f; LP_3		
	SD-1327 g; LP_4		
	SD-1327 h; LM_1		
	SD-1327i; LM_2		
Adult 6			
Upper dentition	SD-1789: RM^2	SD-1654; RP^3	SD-311; LI^1
	SD-1603: RM^3	SD-2158; LM^2	SD-1161; LC
	SD-1833: RM^1	SD-2007; LM^1	
	SD-2040; RP^4		
Lower dentition	SD-1577; LM_1	SD-303; LP_4	SD-406; RM_3
		SD-1575; LP_3	
		SD-753; LC	
		SD-1574; LI_2	
		SD-926; LI_1	
Adult 7			
Upper dentition		SD-407; LM^1	SD-1707; RI^2
			SD-582; RI^1
			SD-639; LP^4
			SD-1164; RM^3
Lower dentition	SD-920; LM_1	SD-936; RM_3	SD-921; RI_2
	SD-928; LM_2	SD-657; RM_1	
Adolescent 1			
Upper dentition	SD-915; LP^4	SD-221; RC	
	SD-913; LC	SD-1106; RP^4	
	SD-916; LM^1	SD-922; RM^1	
	SD-914; LP^3		

Table 1 (*Continued*)

	Level 1	Level 2	Level 3
Lower dentition	SD-780; LM_1	SD-736a; RP_4	SD-755; RM_2 SD-1019; RI_2 SD-278; RI_1 SD-927 RP_3
Adolescent 2			
Upper dentition	SD-411; LP^4 SDR-012; LM^1	SD-1105; RM^1 SD-551; RM^2 SD-621; RM^3 SD-741; LM^3 SD-930; LM^2 SD-50; RP^4	SD-566; RP^3 SDR-013; RI^2 SD-331a; RI^1 SD-331b; LI^1
Lower dentition	SD-756; LM_1 SD-540; LM_2	SD-1510; LM_3 SDR-015; RM_1 SD-924; RM_3	SD-370b; RI_2 SD-918; RC SD-1513; LP_3
Adolescent 3			
Upper dentition	SD-1221; LP^4	SD-1107; LC SD-1075; LP^3 SD-332; LM^3 SD-772; RM^3 SD-568; LI^2 SD-277; LI^1	SD-4; LM^2
Lower dentition	SD-500; LP_4 SD-912; LP_3 SD-61; LC	SD-501; RP_4	
Juvenile 1			
Upper dentition	SD-768; dRm^2 SD-531; RM^1 SD-1862; LM^1 SD-1863; LM^2[a] SD-1824; RP^4[a] SD-2020; RP^3[a] SD-1720; RC[a] SD-1721; dRc **SD-1875; RI^1** **SD-1719; LI^1** **SD-1881; LI^2**[a]		
Lower dentition	SD-1600b; LM_1 SD-1600c; dLm_2 SD-1600d; dLm_1 SD-1600e; dLc SD-1600f; LI_2[a,b] SD-1600 g; LC[a,b] SD-1600 h; LP_3[a,b] SD-1600i; LP_4[a,b] SD-1600j; LM_2[a,b] SD-1660b; RM_1 SD-1660c; dRm_2 SD-1660d; dRm_1 SD-1660e; dRc SD-1660f; RI_1 SD-1660 g; RI_2[a,b] SD-1660 h; RC[a,b] SD-1660i; RP_3[a,b] SD-1660j; RP_4[a,b] SD-1660k; RM_2[a,b] SD-1716; dRi_2 SD-322; LI_1		

Specimens in bold are associated among them at a level 1. The elements found *in situ* are underlined.

[a] Unerupted tooth.

[b] Tooth included in the alveolar bone.

In the specific case of the El Sidrón sample, the reference tooth is represented by the lower left first molar (LM_1; $n = 10$) for the mandibular dentition and by the upper right first molar (RM^1; $n = 9$) for the maxillary one.

2.2.2. Criteria for tooth associations

Given the characteristics of the sample, 12 criteria were considered for tooth association, and a hierarchical classification of their reliability was established. The criteria

Table 2
Summary of individuals and dental associations identified at El Sidrón.
Tableau 2
Tableau synthétique des individus et des associations dentaires identifiés à El Sidrón.

Individual	Reference tooth/bony element	Associated skeletal specimens	Dental associations			Age	Sex
			Lower dentition	Upper dentition	Total		
Adult 1	Left M_1	Mandible (SDR-005, SDR-006, SD-550a) and maxilla (SD-1200a)	3 isolated and 12 *in situ* teeth	9 isolated and 4 *in situ* teeth	28	Young adult	Male
	SDR-005a		8 right; 7 left	5 right; 8 left			
Adult 2	Left M_1	Hemi mandible (SDR-007, SDR-008), mandibular fragments (SD-30,	2 isolated and 8 *in situ* teeth	3 isolated and 13 *in situ* teeth	26	Young adult	Male
	SDR-007d	SD-1095a) and maxilla (SD-1427a)	2 right; 8 left	8 right; 8 left			
Adult 3	Left M_1	Hemi mandible (SD-1217a, SD-1218) and maxilla (SD-2200)	2 isolated and 8 *in situ* teeth	1 isolated and 5 *in situ* teeth	16	Mature adult	Female
	SD-1217e		5 right; 5 left	5 right; 1 left			
Adult 4	Left M_1	Fragment of mandible (SD-599) and fragment of maxilla (SD-1683)	11 isolated and 2 *in situ* teeth	9 isolated and 2 *in situ* teeth	24	Young adult	Female
	SD-331c		6 right; 7 left	6 right; 5 left			
Adult 5	Left M_1	Dental row found *in situ* and maxilla	9 teeth *in situ*	16 teeth *in situ*	25	Mature adult	Female
	SD-1327 h	(SD-2010)	2 right; 7 left	8 right; 8 left			
Adult 6	Left M_1	Maxillary fragment (SD-1789)	7 isolated teeth	8 isolated and 1 *in situ* teeth	16	Mature adult	Male
	SD-1577		1 right; 6 left	5 right; 4 left			
Adult 7	Left M_1		5 isolated teeth	5 isolated teeth	10	Mature adult	?
	SD-920		3 right; 2 left	3 right; 2 left			
Adolescent 1	Left M_1	Small maxillary fragment (SD-917)	6 isolated teeth	3 isolated and 4 *in situ* teeth	13	Adolescent approx. 11-12 years	Male
	SD-780		5 right; 1 left	3 right; 4 left			
Adolescent 2	Left M_1	Small mandibular fragment (SD-1510) and small maxillary fragment	1 isolated and 7 *in situ* teeth	10 isolated and 2 *in situ* teeth	20	Adolescent	?
	SD-756	(SD-331a, SD-331b)	4 right; 4 left	7 right; 5 left		Approx. 12-13 years	
Adolescent 3	Left P^4	Small mandibular fragment (SD-912)	3 isolated and 1 *in situ* teeth	8 isolated teeth	12	Adolescent	Male
	SD-1221		1 right; 3 left	1 right; 7 left		Approx. 12-13 years	
Juvenile 1	Left M_1	Mandible (SD-1600a, SD-1660a, SD-2009), small maxillary fragment	2 isolated and 19 *in situ* teeth	10 isolated and 1 *in situ* teeth	32[a]	Juvenile	Male
	SD-1600b	(SD-1875) and postcranial elements	11 right; 10 left	7 right; 4 left		Approx. 7.5 years	
Juvenile 2	Ulna	Postcranial elements				Juvenile	?
	SD-763b					Approx 9-10 years	
Infant 1	Tibia	Postcranial elements				Infant 2-3 years	?
	SDR-157						

[a] Mixed dentition includes deciduous and permanent elements, both complete and/or in formation (see Table 1 for detailed information).

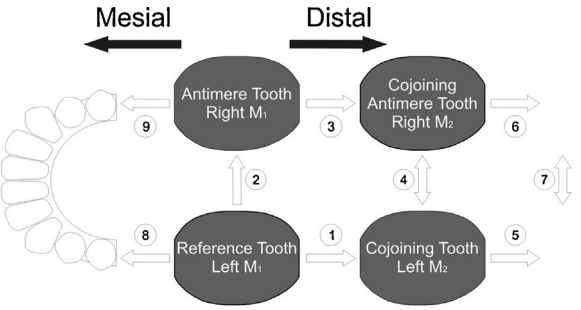

Fig. 1. Scheme for the lower dentition of the procedure followed for establishing tooth association in the El Sidrón Neandertal sample. 1: association of the element distally cojoining the reference tooth, i.e., the LM_2; 2: identification of the antimere of the reference tooth, i.e., the RM_1; 3: association of the element distally cojoining the antimere of the reference tooth, i.e., the RM_2; 4: testing the congruence between the results of steps 1 and 3; 5: association of the next contiguous tooth along the left row, i.e., the LM_3; 6: association of the next contiguous tooth along the right row, i.e., the RM_3; 7: testing the congruence between the results of steps 5 and 6. Once completed the assessment along the distal direction, the same procedure is followed in mesial direction, starting with (8) the association of the element proximally cojoining the reference tooth, i.e., the LP_4 and (9) of the element proximally cojoining the antimere of the reference tooth, i.e., the RP_4.

Fig. 1. Schéma, pour la denture inférieure, de la procédure adoptée pour établir les associations dentaires dans l'échantillon néandertalien d'El Sidrón. 1 : association de l'élément correspondant distalement à la dent de référence, i.e., la LM_2 ; 2 : identification de l'antimère de la dent de référence, i.e., la RM_1 ; 3 : association de l'élément correspondant distalement à l'antimère de la dent de référence, i.e., la RM_2 ; 4 : contrôle de la compatibilité entre les résultats des étapes 1 et 3 ; 5 : association de la dent suivante le long de la rangée dentaire gauche, i.e., la LM_3 ; 6 : association de la dent suivante le long de la rangée dentaire droite, i.e., la RM_3 ; 7 : contrôle de la compatibilité entre les résultats des étapes 5 et 6. Une fois complétées, les associations en direction distale, la même procédure est suivie en direction mésiale, à commencer par (8) l'association de l'élément correspondant proximalement à la dent de référence, i.e., la LP_4 et (9) de l'élément correspondant proximalement à l'antimère de la dent de référence, i.e., la RP_4.

below are listed in decreasing order of relevance, with the first six being the most relevant:

1. the anatomical connection (either based on the existence of a skeletal support or the topographic distribution at the site);
2. the exact fitting of a tooth in its alveolar socket;
3. the matching of interproximal wear facets:
   In order to establish a link between two isolated teeth, one of the criteria used in this study is the similarity between adjacent interproximal wear facets (Fig. 2) (Benazzi et al., 2011; Gençturk et al., 2008; Poisson et al., 2002; Rosas et al., 2006; Villa and Giacobini, 1995; Wolpoff, 1979, among the others). Apart from the size and shape of the facets, we principally considered the pattern of subvertical grooves when present. As often seen in Neandertal samples (Egocheaga et al., 2004; Poisson et al., 2002; Villa and Giacobini, 1995), a high frequency of subvertical grooves is also found in El Sidrón (Estalrrich et al., 2011). These are disposed in well-defined patterns that allow individual identification, precisely because there are no two equal subvertical groove patterns in the sample. By using scanning electron micrographs, the similarity between two presumably adjacent facets is tested by superimposing (using Adobe Photoshop©) the features of the mesial facet to the scaled and mirrored outline of the distal facet, including its subvertical grooves if present (Fig. 2). If the facets are alike, the teeth are considered to be a match;
4. the degree of occlusal wear (Skinner, 1997);
5. the developmental age and eruption stage (AlQahtani et al., 2010);
6. the tooth crown and root morphology.

This criterion is especially used for antimere identification. For size assessment, we used the bucco-lingual (BL) and mesio-distal (MD) diameters, the size and location of the cusps and crests, as well as other morphological details scored according to the ASUDAS system (Turner II et al., 1991).

There are additional criteria which have also been considered on a case by case basis. These include: 7: lineal or pitted enamel hypoplasia; 8: presence, abundance and location of dental calculus; 9: various biological features and oral pathologies (Prieto, 2005; Dean et al., 2013); 10: chipped enamel (following the score procedures by Belcastro et al., 2004); 11: pattern and abundance of instrumental or cultural striations (scratches on the labial surface of the anterior dentition related to para-masticatory activities; Bermúdez de Castro et al., 1988; Frayer et al., 2010, among the others; for El Sidrón, see Estalrrich and Rosas, 2013); 12: taphonomic features (e.g., colour, similarity in the superficial covering of calcareous deposits, etc.).

All dental macro- and micro-features were analyzed and assessed using binocular lens, optical microscope (Olympus© BX51) and ESEM (Fei Quanta 200©).

2.2.3. Degree of reliability of the associations

In order to better control error distribution of the associations, the degree of reliability regarding the attribution of a new tooth to a specific individual or to an anatomically-related set of dental remains has been established based on three levels of confidence (Table 1). Firstly, for practical reasons, we considered all unequivocal associations as "level 1" (criteria 1 and 2). Then, when tooth association satisfied three or more major criteria, the reliability was scored as "level 2". Finally, "level 3" indicates tooth attributions in which three or less of the major criteria were satisfied or associations relying on a process of elimination. Additional criteria help to clarify or reinforce the degree of reliability (level of the association).

When the association of a tooth to a dental row was not evident (insufficient number of matching criteria), we have considered it more parsimonious to leave the specimen unassociated rather than to create a new unit. When possible, we tried to find a correlation between an unassociated specimen and the previously identified individuals, always taking into account the greatest number of minor criteria ("level 3" of reliability).

2.2.4. Criteria for matching upper and lower dentitions

Occlusal fit is the principal criterion used for matching upper and lower dentitions. Additionally, secondary criteria include dental wear pattern, developmental age,

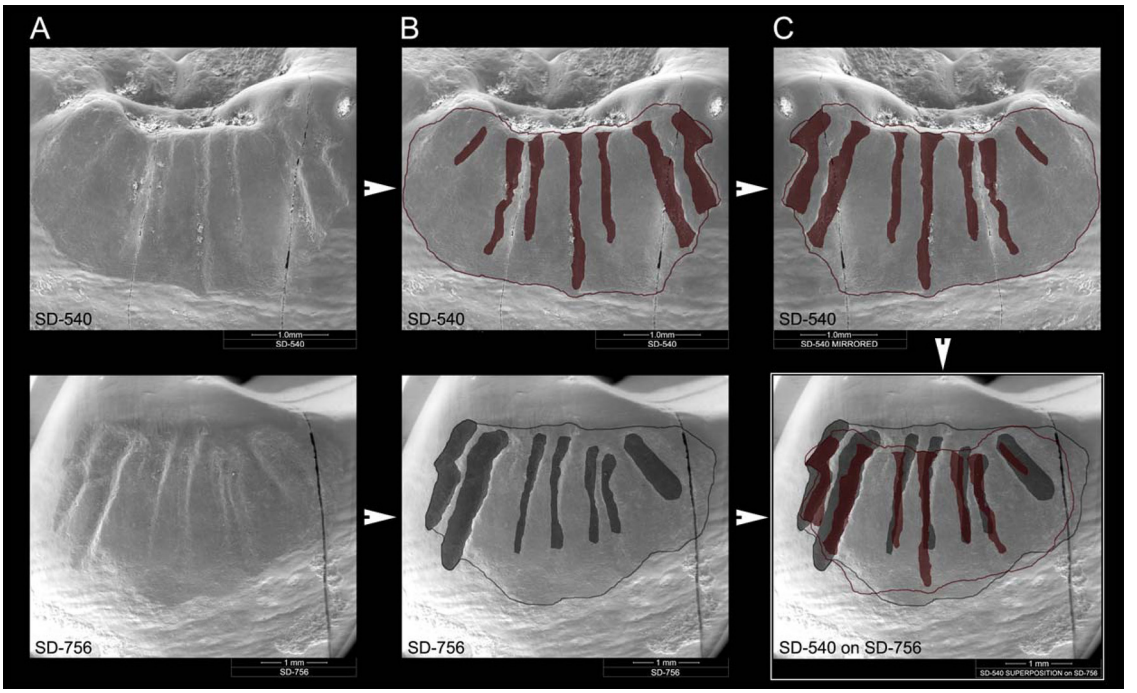

Fig. 2. Superposition of conjoint interproximal wear facets. ESEM micrographs of (A) the distal interproximal facet on the LM_1 (bottom) and the mesial facet of the LM_2 (top). B. Outlines of the two interproximal facets and of the subvertical grooves. C. Superposition of the scaled, rotated and mirrored LM_2 mesial facet outlines to the LM_1 distal figures.
Fig. 2. Superposition de facettes d'usure interproximales correspondantes. Micrographie ESEM de (A) la facette interproximale distale de la LM_1 (en bas) et de celle mésiale de la LM_2 (en haut). B. Contours des deux facettes interproximales et des sillons subverticaux. C. Superposition sur l'image de la facette distale de la LM_1 des contours de la facette mésiale de la LM_2 après étalement, rotation et effet miroir.

presence of hypoplasia lines, presence of dental calculus, colouring pattern, and texture features.

3. Results

A minimum of 13 Neandertal individuals have been identified in the El Sidrón fossil sample. Eleven of them were defined from the permanent dentition: seven adults, three adolescents and a juvenile, the latter represented also by deciduous tooth elements (Fig. 3; Tables 1 and 2). Two additional individuals, one infant and another juvenile, were determined only from postcranial remains.

3.1. Lower dentition

In the assemblage, the permanent lower left first molar (LM_1) is the most represented dental element indicating an MNI of ten (Table 2). Accordingly, the M1s have been used as reference units for assembling other isolated teeth (see methods). Amongst them, four are preserved in their respective mandibles (Adult 1 to 3 and Juvenile 1). In addition, Adult 5 was discovered during the excavations associated with a dental row consisting of 9 additional teeth (Tables 1 and 2). All but one LM_1 are fully developed and present different stages of occlusal wear (from 0 to 4–5), the remaining one, which exhibits an unfused root apex, identifies the individual Juvenile 1.

During the process of successive association of the mandibular teeth, a new individual was identified (Adolescent 3) using a set of unmatched lower teeth. Using this matching process based on the permanent mandibular teeth, eleven individuals have been identified. The age assessment of the seven adults is based on the presence of fully erupted and variably worn third molars (in six cases) and the presence of an interproximal distal wear facet on the second mandibular molar (Adult 5). Two dental assemblages are identified as adolescent individuals. The assessment of Adolescent 1 is based on the presence of a second molar lacking the interproximal distal wear facet and showing only a low degree of occlusal wear (stages 1 and 2), while Adolescent 2 is identified by an unerupted third molar (SD-1510). The tooth set that was not possible to associate with any of the reference M_{1s} (Adolescent 3) presents a slight occlusal wear (stages 1 and 2) similar to that found in the aforementioned adolescents. All of the above evidence based of the permanent tooth elements allows the identification of eleven individuals, further confirmed by the analysis of the upper dentition (see below).

3.2. Upper dentition

Among the maxillary teeth collected at El Sidrón, the upper right first molar (RM^1) is the most represented element with nine specimens recovered, four being *in situ* and five isolated (see Tables 1 and 2 and Fig. 3). One RM^1 having unclosed roots indicates the presence of a minimum of nine tooth associations. During the upper teeth

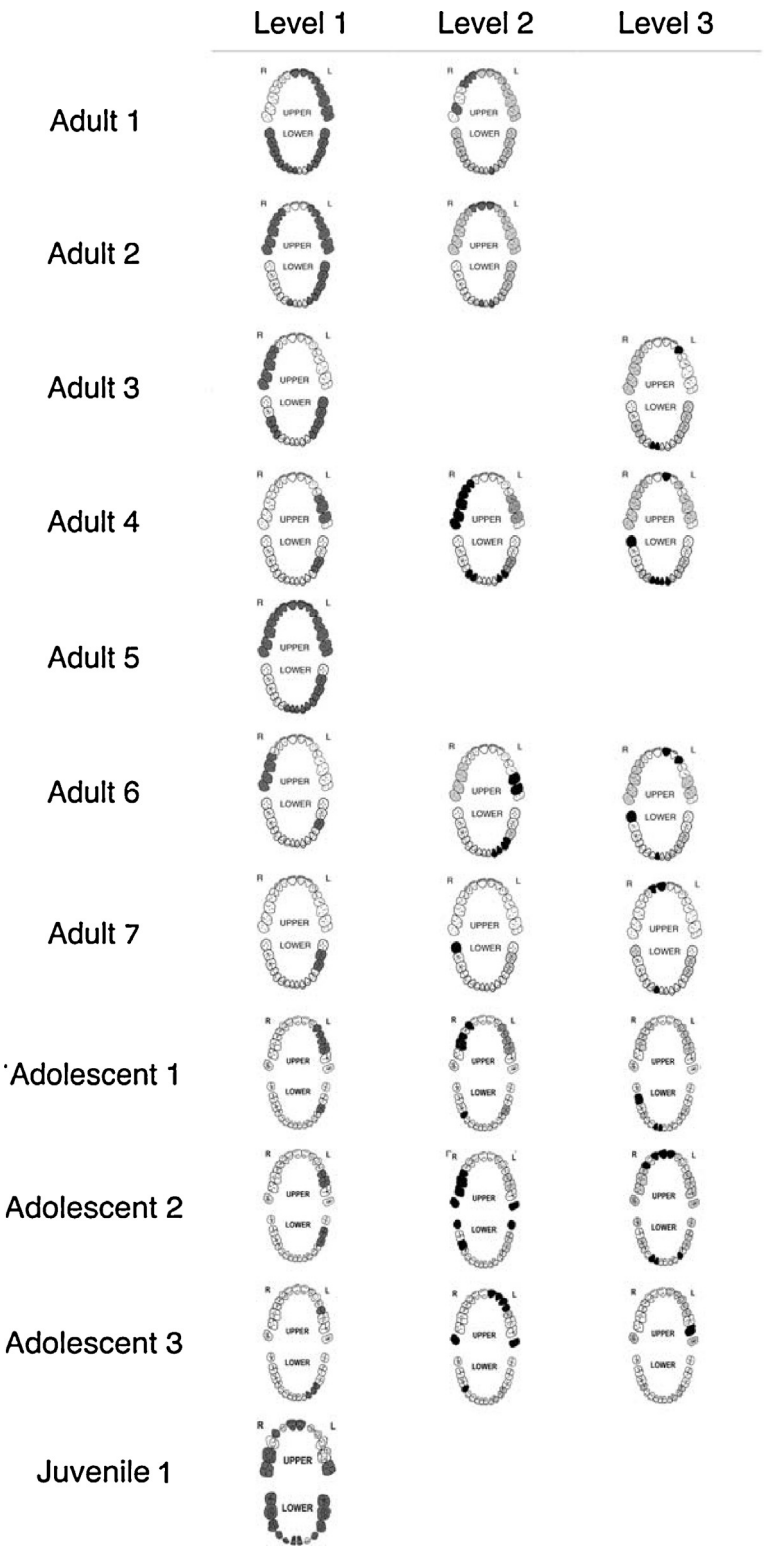

Fig. 3. Tooth associations in the El Sidrón Neandertal sample defining 11 of the 13 individuals identified so far. The different dental elements are progressively associated to the reference teeth (LM_{1s}) following three levels of reliability. See text for the description of the three levels.
Fig. 3. Associations dentaires dans l'échantillon néandertalien d'El Sidrón indiquant 11 des 13 individus identifiés à ce jour. Les différents éléments dentaires sont associés progressivement aux dents de référence (LM_{1s}) selon trois niveaux de fiabilité. Voir le texte pour la description des trois niveaux.

association process, two additional individuals were identified increasing the total number of associations to eleven.

Seven dental sets are attributed to adult individuals based on: tooth wear (stages 4 and 5), M^3 adscription (six RM^3 are completely developed and show occlusal wear) and the presence of M^2 distal wear facet. We named these individuals Adult 1 to Adult 7 (Fig. 3; Tables 1 and 2). Based on the beginning stage of root formation of two upper left third molars (LM^3) and two right third molars (RM^3), two sets were attributed to adolescent individuals. Another assemblage (left C to M^1 found in association at the site) shows a degree of occlusal wear compatible with an adolescent age (stages 1 and 2) (Table 1 and Fig. 3). The presence of a left P^4 already represented in both previously identified adolescents indicates a new individual (Adolescent 1).

Finally, another maxillary row is represented by a RM^1 with its root still under formation. While this tooth was found isolated, it can be associated to 10 additional teeth (including deciduous elements and premolar germs) based on their developmental stage (Tables 1 and 2).

3.3. Matching of the lower and upper dentitions

Occlusal fitting criteria of the permanent elements and the combination of the upper and lower dental associations indicate the presence of 11 individuals, whereas relative dental wear and developmental criteria had already defined seven adults. The remaining three individuals are defined as follows. Adolescent 1 is defined by one adolescent mandibular assemblage (RM_2 without distal wear facet; SD-755) fitting the maxillary assemblage displaying low occlusal wear. Adolescent 2 is defined by a second adolescent mandibular set (unerupted left M_3; SD-1510) fitting a similarly identified maxillary assemblage with incomplete M^3 roots. Finally, Adolescent 3 is represented by the mandibular assemblage displaying a low degree of occlusal wear which fits the last maxillary set compatible with an adolescent (M^3s with roots at a premature formation stage) (Fig. 3; Tables 1 and 2).

An additional juvenile individual, Juvenile 1, with which a number of postcranial elements can be securely associated (Fig. 3), has been defined by the presence of a complete mandible bearing a mixed dentition which, due to its developmental stage, cannot be assigned to any of the previously identified individuals. Duplication of postcranial elements such as ulna, radius and right V metacarpal of an immature specimen older than Juvenile 1 (following Scheuer and Black, 2000) requires the presence of Juvenile 2, a second juvenile individual. Lastly, despite a lack of any dental remains, the presence of a 1.5–3-year-old infant has been identified using a distal fragment of a right tibia (Egocheaga and Sierra, 2005; Rosas et al., 2006), a right hallux and a fifth metatarsal.

In summary, a minimum of 13 Neandertal individuals have been identified within the El Sidrón fossil assemblage. It should however be noted that an isolated slightly worn RI^2 (SD-536b) preserving its lingual crown side but not the root, cannot be associated with any of the individuals identified so far.

4. Discussion

Until the 2005 field season, eight Neandertal individuals had been identified at El Sidrón (Rosas et al., 2006). Since then, the dental sample has considerably increased and a more systematic and consistent approach for assessing the MNI has been adopted, increasing to 13 the number of ascertained individuals.

The process of tooth sequential association is greatly affected by differential tooth preservation conditions usually affecting each quadrant of the dentition. At El Sidrón, the elements from the lower dentition, notably from the left side ($n = 61$), are better represented across the individuals, while the elements of the upper dentition are essentially concentrated in five out of the 11 identified individuals. Also, the lack of maxillary elements in some dental sets (in Adult 7 and Adolescent 3) precludes a high degree of verisimilitude in upper-lower row associations.

In the assessment of the MNI in human fossil assemblages, a number of error sources can be assumed *a priori*. It is noteworthy to mention those related to the anatomical identification of dental specimens. For example, mostly due to the variable frequency of additional cusps and crests expressed at the outer surface, an unequivocal distinction between isolated M_1–M_2 and M_2–M_3 is not possible in Neandertal samples (Bailey and Hublin, 2006; Lebel and Trinkaus, 2002; Lebel et al., 2001; Maurielle et al., 2008). Nonetheless, at El Sidrón the size of the distal molar cusp (entoconid or hypoconulid) allows reliable identifications that, at least in some cases, are also supported by evidence from the interproximal facet matching (Fig. 2).

Occlusal wear asymmetry in hunter-gatherer populations (Deter, 2009; Merbs, 1983; Molnar, 1972; Molnar et al., 1983; Puech, 1981) is another source of error, especially in the case of antimere identification. Also, because it increases the difficulty of associating anterior and posterior dentitions, the commonly advanced and group-specific degree of anterior tooth wear typical of Neandertals deserves attention (Lozano et al., 2008; Puech, 1981; Ungar et al., 1997; Wallace, 1975).

Sex attributions are usually based on canine size, the most dimorphic tooth in humans and other primates (Bermúdez de Castro et al., 1993, 2001; Leutenegger, 1982; Leutenegger and Kelly, 1977; Thorén et al., 2006), as well as on mandibular size and shape. Paleogenetic evidence at El Sidrón based on Y-chromosome markers has confirmed 100% of previous sex attributions performed on morphological grounds (Lalueza-Fox et al., 2011). However, additional skeletal sites and further genetic tests still have to be considered for sexing the still unknown individuals and providing a more robust picture of the composition per sex of this Neandertal group. Similarly, age estimations have been performed so far in the perspective of tooth association. Accordingly, seven individuals presenting a moderate degree of dental wear have been identified, the maximum corresponding to stages 5-6 (Skinner, 1997). However, no cases of extreme dental wear (senile individuals) have been recorded in the sample.

Excavations at El Sidrón are planned for the coming years, and it is likely that new human specimens will be recovered in the near future. Hopefully, new material and

new analyses will complete and enlarge the number of individuals reported in this study. In this perspective, a next step in our investigation will be the attribution of the isolated postcranial elements to the individuals defined on dental criteria.

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Brief Communication: Subvertical Grooves on Interproximal Wear Facets From the El Sidrón (Asturias, Spain) Neandertal Dental Sample

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ABSTRACT The distribution of subvertical grooves on interproximal wear dental facets from the El Sidrón (Asturias, Spain) Neandertals is described and analyzed. Out of 93 teeth, 64.5% present subvertical grooves, including a high frequency (50%) on the anterior dentition. Contrary to some studies, subvertical grooves from adjacent facets perfectly overlap each other and do not interdigitate, probably forming small channels. Both the facet and the groove surface share the same polished appearance, suggesting a common origin. Statistical analyses reveal that the number of grooves is neither dependent on the degree of occlusal wear, nor on the position on the tooth or the individual's age. However, facet width is an important factor determining the number of subvertical grooves. The etiology of subvertical grooves formation on Neandertal teeth remains unclear. Am J Phys Anthropol 144:154–161, 2011.

Subvertical grooves are small furrows located on the interproximal wear facets [the latter caused by tooth-to-tooth contact (Wolpoff, 1971; Lucas, 2004)], and they usually display a subvertical orientation radiating from the occlusal surface (hence the name). Subvertical grooves are semicircular in cross-section and appear from one to eight in number and 0.1–0.5 mm in width (Villa and Giacobini, 1995).

Subvertical grooves have been observed primarily in the permanent posterior dentition of *Homo neanderthalensis* [Figueira Brava, Fate, Rochelot, Genay, and El Sidrón (Giacobini et al., 1984; Antunes and Santinho Cunha, 1992; Villa and Giacobini, 1995; Poisson et al., 2002; Egocheaga et al., 2004; Rosas et al., 2006)]. This trait has also been described in other fossil and extant hominins, such as *H. habilis* [Omo Valley (Puech and Cianfarani, 1988)], Atapuerca-SH *H. heidelbergensis* (Pérez-Pérez et al., 2003), early modern humans [Qafzeh (Vandermeersch, 1981)], and modern humans [Australians and Europeans, (Kaidonis et al., 1992)].

Despite these previous descriptions, corresponding grooves on adjacent teeth were noted only on three Neandertal tooth pairs from Genay (Villa and Giacobini, 1995) and on one pair of premolars from Rochelot (Poisson et al., 2002). In addition, subvertical grooves have occasionally been detected in the anterior dentition, such as on one incisor from Genay (Villa and Giacobini, 1995), two canines from Rochelot—although they are reported as atypical—(Poisson et al., 2002), and in a few cases in the El Sidrón sample (Rosas et al., 2006).

Several authors (Villa and Giacobini, 1995; Poisson et al., 2002) proposed a sequential model for the origin of the subvertical grooves. According to Villa and Giacobini (1995), Neandertal teeth sustained high levels of force during chewing, such that vertical cracks would occur in the inner enamel. In the case of Neandertals as compared to modern humans, the vertical cracks were not stopped by the Hunter-Schreger bands (HSB), which present a subvertical disposition among them. The wearing down of the interproximal facets would reach these vertical cracks, which were then exposed on the facet surface. After that, microcracks would have been worn by abrasion but mainly by chemical erosion, giving rise to the primary subvertical grooves. These authors, nevertheless, noted that microcracks are visible within the grooves in only a few cases. Packing of exogenous acid material into the microcrack could have been responsible for the formation by chemical erosion of a mirroring groove on the adjacent facet.

Poisson et al. (2002) proposed a variation of the previous model in which the formation of an interproximal wear facet appears prior to the appearance of the microcracks: the worn interproximal enamel then becomes less resistant and favors the formation of these microcracks.

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This nuanced model also considers that the widening of a microcrack furrow to a primary subvertical groove and the enlargement of the secondary mirrored groove were caused not only by chemical erosion, but mainly by mechanical forces.

The aims of this brief communication are to document the subvertical grooves on both the anterior and posterior dentition of the El Sidrón Neandertals and to explore the congruence of these data with previously proposed hypotheses about their etiology.

MATERIALS AND METHODS

The El Sidrón site (Asturias, Northern Spain) is located in a small gallery (Galería del Osario) belonging to the El Sidrón karst system (Rosas and Aguirre, 1999; Fortea et al., 2003; Rosas et al., 2006). Sediments are mostly sands and clays, with gravel layers indicating variations in hydraulic energy (Fortea et al., 2003; Rosas et al., 2006; Santamaría et al., 2010).

More than 1700 skeletal remains have been recovered, all the skeletal parts are represented, and some of the remains are in anatomical connection (Rosas et al., 2006). There is a moderate occurrence of Middle Paleolithic stone tools, and few faunal remains. The age of the bone assemblage has been estimated at ~49 kya (Torres et al., 2010).

Up until 2008 field season, the total dental sample from El Sidrón comprises 145 specimens belonging to a minimum number of individuals (MNI) of 11, including adults, adolescents and juveniles. Out of that sample, seven specimens are root fragments, 37 teeth are found in their respective alveoli (and it was not possible to observe their interproximal wear facets with conventional methods), and three canines and five molars are unerupted teeth. The dental sample analyzed in this study therefore comprises 93 teeth: 32 incisors, 10 canines, 23 premolars, and 28 molars. Among them, there are nine tooth pairs that allowed studying the mode in which adjacent interproximal facets contact. Those teeth were found in anatomical connection but without bony support, or belong to refitted mandible fragments. Those tooth pairs are associated to adult individuals.

Interproximal wear facets and subvertical grooves can be seen with the naked eye, but we used a binocular microscope (Leica S6D®, up to 40×, equipped with a Canon® camera) to verify the morphology. We further employed an Environmental Scanning Electron Microscope (ESEM, Fei Quanta 200®) in low vacuum mode, in secondary emissions mode and an accelerating voltage of 20 kV. Once the tooth was correctly placed (the interproximal facet perpendicular to the electron beam inside the microscope chamber), several micrographs were taken at different magnifications. A general view of 25× to 40× depending on the size of the facet, a more detailed view of the grooves at 100×, and in those cases where the groove was well defined, another series of micrographs (at higher magnification levels) were taken with the purpose of exploring the bottom of the groove and looking for traces regarding its origin [i.e., the microcracks observed by Villa and Giacobini (1995)].

Different measurements were taken from the micrographs to characterize facet morphology: width and length (only when occlusal wear was minimal), as well as width (at the most occlusal end, in the middle, and at the most cervical end), length and depth of the grooves, when possible. Measurements were quantified using ImageJ 1.33u (Rasband, 1997–2006).

In some cases, it was necessary to make high-resolution casts of the teeth, because the bone fragments accompanying them were too big for the microscope chamber dimensions. For this purpose we followed the procedure proposed by Bromage (1987), employing a hydrophilic vinyl polysiloxane impression material (Exaflex®) to make the negative cast and a polyurethane resin (Feropur®) to make the positive cast. The positive mold was coated with gold (sputter coater EMYTECH®) to allow the ESEM observation.

To examine the cross-section of the groove, high-resolution negative casts of the interproximal facets were made, then cut perpendicularly to their main axes and explored under the microscope.

General Linear Models (GLM) analyses were applied in order to explore the relationships between the number of subvertical grooves on an interproximal wear facet, and some biological characteristics associated with the tooth (e.g., individual age, occlusal dental wear, facet width, and its position on the tooth). The category of "individual" was selected as a random factor. GLM is a generalization of the linear regression model, such that effects can be tested for categorical as well as continuous predictor variables and in designs with multiple dependent variables.

RESULTS

The El Sidrón subvertical grooves appear as small furrows and semicircular shape in cross-section. In most of the cases, the grooves contact at least one of the margins of the facet (occlusal or cervical), more often the occlusal one. However, in four cases of the 109 studied facets, the grooves do not contact any of the facet margins. The orientation of the grooves is mainly radial, diverging from the occlusal border of the facet. The shape of the grooves varies, ranging from straight to slightly curved, "S" shaped and zigzag. The facet shape most frequently found was flat (73% of the total facets with grooves), followed by concave (14%) and convex (13%) (Table 1).

Presence and distribution of subvertical grooves

Sixty out of 93 teeth (64.5%) present at least one groove on one of their facets. We observed 85 interproximal wear facets with subvertical grooves. Fifty percent of the anterior teeth present subvertical grooves, of which 15 are incisors (see Fig. 1) and 6 are canines (see Fig. 2). This is an important finding because subvertical grooves have been previously observed mainly in the posterior dentition. Of the 51 premolars and molars, 39 teeth (76.5%) have subvertical grooves (Figs. 3 and 4).

The number of grooves per facet varies from one to four on the incisors and from one to five on the canines (Table 1). On the posterior dentition, the number of grooves ranges from one to eight (see Fig. 4). The facets with the largest number of grooves (seven and eight grooves per facet) were the distal ones on the P_4s, the mesial and distal on the M_1s, and mesial on the M_2s (Table 1).

Characteristics of subvertical grooves

The width, length, and depth of the grooves vary depending on the tooth type (Table 2). The longest grooves are on the incisors, whereas the widest and deepest grooves are on the molars. Generally, the width

TABLE 1. List of the subvertical grooves found on the interproximal wear facets from the El Sidrón dental sample

Specimen and tooth	Occl. wear[a]	Mesial No. grooves	Mesial facet width (mm)	Mesial Shape	Distal No. grooves	Distal facet width (mm)	Distal Shape
SD-1106; RP^4	2	2	4.53	Flat	1	3.91	Convex
SD-763a; RP_4	2	2	2.61	Flat	4	2.67	Flat
SD-780; LM_1	2	3	2.52	Flat	0	3.23	Flat
SD-566; RP^3	2	0	0.92	Flat	2	2.96	Concave
SD-50; RP^4	2	1	1.86	Flat	4	2.26	Flat
SD-1105; RM^1	2	3	5.00	Flat	3	4.13	Convex
SD-551; RM^2	2	1	2.91	Flat	None	None	None
SD-331b; LI^1	1	0	1.30	Flat	2	1.79	Concave
SD-411; LP^4	2	5	3.78	Flat	0	2.06	Flat
SDR-012; LM^1	2	7	5.78	Flat	1	3.04	Flat
SDR-015; RM_1	2	8	5.25	Flat	6	4.04	Flat
SD-756; LM_1	2	3	4.20	Flat	7	4.20	Flat
SD-540; LM_2	2	7	4.71	Flat	None	None	None
SD-568; LI^2	2	2	2.14	Flat	0	2.27	Flat
SD-1221; LP^4	2	0	2.62	Flat	2	3.04	Flat
SD-501; RP_3	2	0	1.55	Flat	1	2.43	Concave
SD-912; LP_3	2	None	None	None	2	2.28	Convex
SD-500; LP_4	2	1	2.48	Flat	1	4.03	Convex
SD-313; RI^1	5	0	3.18	Flat	1	1.81	Concave
SD-1010; RC^1	5	None	None	None	1	2.33	Flat
SD-1054; RM^1	6	3	5.76	Flat	0	5.58	Flat
SD-1201; LI^1	5	1	1.59	Flat	0	1.33	Flat
SD-441; LI^2	5	2	1.68	Flat	0	2.04	Flat
SD-1202; LC^1	5	0	1.45	Concave	1	1.87	Flat
SD-312; LP^3	5	0	3.11	Flat	1	3.01	Flat
SD-1200a; LP^4	5	0	2.29	Concave	2	3.12	Convex
SD-1200b; LM^1	5	2	6.89	Concave	4	5.15	Convex
SD-1200c; LM^2	5	4	6.03	Concave	None	None	None
SD-1135; RM_3	5	1	3.47	Flat	None	None	None
SD-664; LP_4	5	3	1.66	Flat	7	4.20	Flat
SD-1422; RI^1	3	2	2.09	Flat	3	2.69	Flat
SD-1240; RI^2	3	0	2.78	Flat	1	2.69	Flat
SD-1439; LI^1	3	2	2.37	Flat	1	1.93	Flat
SD-703; RI_1	4	2	2.40	Concave	0	1.71	Flat
SD-1220; LC^1	6	3	1.76	Convex	0	2.07	Flat
SD-1216a; RP_3	6	0	1.69	Flat	7	3.29	Concave
SD-1216b; RP_4	6	6	3.37	Convex	2	4.59	Flat
SD-1216c; RM_1	6	3	4.83	Flat	8	4.85	Flat
SD-1217c; LP_3	6	0	2.84	Flat	1	3.60	Concave
SD-1217d; LP_4	6	1	3.63	Convex	None	None	None
SD-1217e; LM_1	6	None	None	None	7	4.14	Convex
SD-1218a; LM_2	6	6	4.57	Concave	5	3.40	Flat
SD-1218b; LM_3	5	4	3.68	Flat	None	None	None
SD-1572; LI^1	4	1	2.75	Flat	2	2.38	Flat
SD-1018; LC^1	3	1	1.58	Flat	0	0.41	Flat
SD-1576; LP^4	4	4	4.00	Flat	2	5.28	Flat
SD-599b; RI_1	3	0	1.96	Flat	2	2.02	Flat
SD-355; RI_2	4	3	2.31	Flat	0	2.36	Concave
SD-331c; LM_1	4	3	5.03	Flat	4	5.48	Flat
SD-406; LM_3	2	4	3.46	Flat	None	None	None
SD-1327e; LC_1	5	1	2.60	Concave	2	2.71	Flat
SD-407; RM^2	6	8	4.90	Flat	None	None	None
SD-311; LI^1	5	4	3.26	Flat	3	1.95	Concave
SD-1161; LC^1	5	0	0.82	Flat	5	3.68	Flat
SD-639; LP^4	5	4	5.62	Flat	6	5.84	Convex
SD-1574; RI_2	4	1	2.13	Flat	0	2.00	Concave
SD-657; RM_2	5	2	4.87	Flat	7	3.81	Concave
SD-303; LM_1	4	1	3.96	Flat	7	4.70	Flat
SD-1577; LM_1	5	8	5.42	Flat	8	4.95	Flat
SD-582; RI^1	4	1	3.20	Flat	0	2.30	Flat

The shadowed rows indicate the pairs of teeth found in situ with subvertical grooves in their interproximal facets.
[a] Occlusal wear degree has been measured following the 8-stage scale proposed by Skinner (1997).

and depth vary along a single groove; grooves are usually wider and deeper on the occlusal end than on the cervical one. In addition, width and depth also vary among the grooves on the same facet.

No microcracks were found at the bottoms of the grooves on any of the teeth. Both surfaces inside the grooves and those of the interproximal facets have the same texture (see Fig. 5).

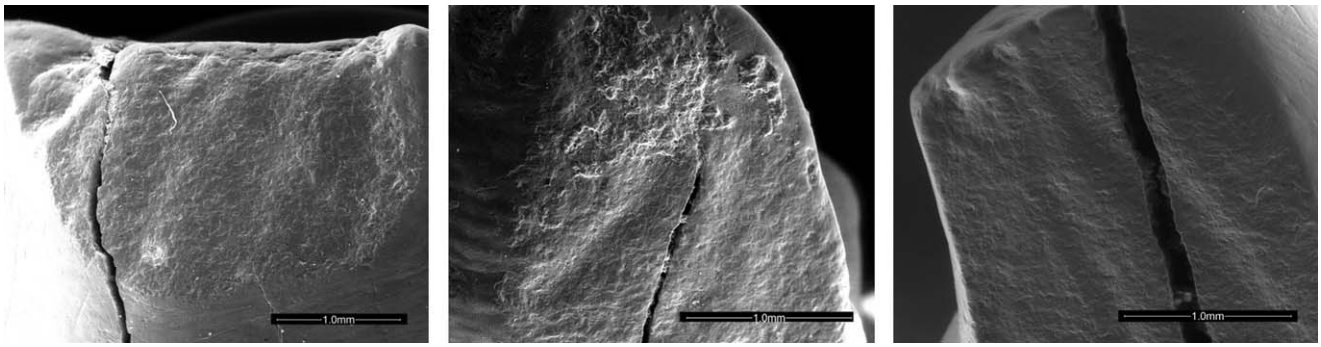

Fig. 1. Subvertical grooves on incisors from the El Sidrón sample. Left: Mesial interproximal wear facet of a left upper incisor (SD-311, LI^1) with 4 subvertical grooves. Middle: Mesial interproximal wear facet of a left upper incisor (SD-568, LI^2) with two subvertical grooves. Right: Distal interproximal wear facet of a right lower second incisor (SD-355, RI_2) with two subvertical grooves.

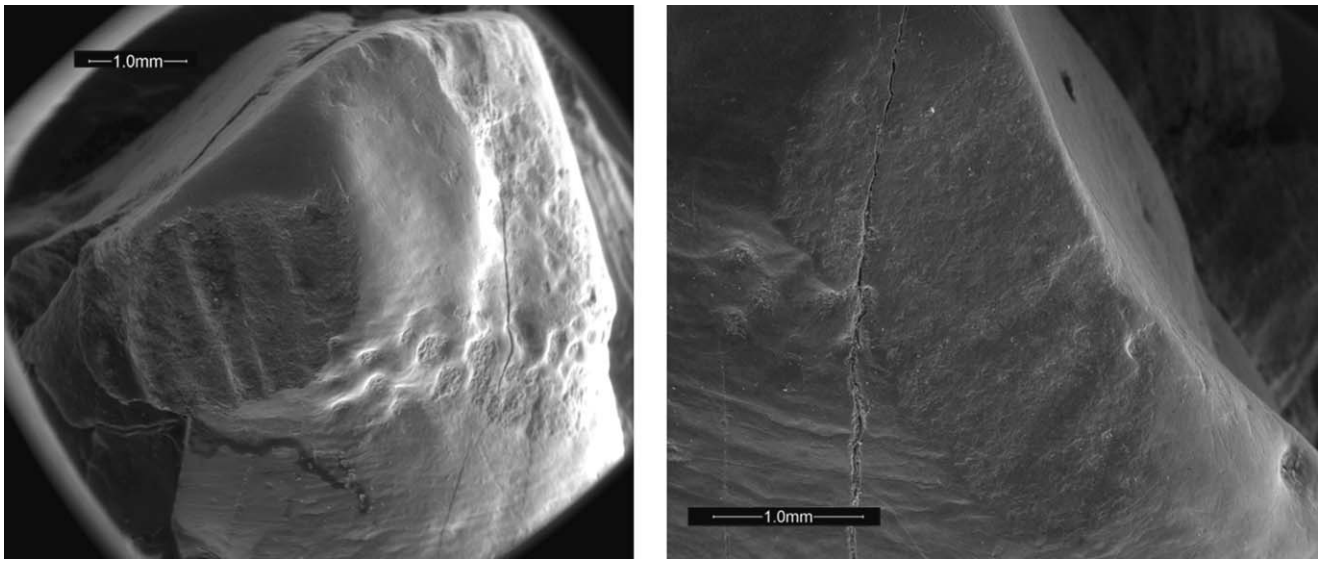

Fig. 2. Subvertical grooves on canines from the El Sidrón sample. Left: Distal interproximal wear facet of a left upper canine (SD-1161, LC^1) with five subvertical grooves. Right: Mesial interproximal wear facet of a left upper canine (SD-1220, LC^1) with three subvertical grooves.

Superposition of cojoining facets by means of micrographs shows a close correspondence between the size and shape of the facets, as well as between the number and distribution of the subvertical grooves. The subvertical grooves from adjacent facets perfectly overlap each other, forming small channels.

Relationship between the number of grooves and tooth characteristics

The GLM indicates that the only significant factor associated with the number of subvertical grooves per tooth is facet width (Table 3). Neither the degree of occlusal wear, nor the mesial or distal position on the tooth, nor the individual age were found to be statistically significantly associated (Table 3). Furthermore, the deepest grooves were found on teeth with slight degrees of occlusal wear [Stages 2–3 of Skinner (1997); see Fig. 4]. The shallowest grooves were found on teeth with a moderate to high degree of occlusal wear (Stages 4–5 of Skinner). The grooves on the distal facet of SD-664 (see Fig. 3) provide an example.

DISCUSSION

Our results show for the first time a high frequency (50%) of appearance of subvertical grooves on the anterior dentition of a Neandertal sample, as well as an elevated incidence on the posterior dentition of the El Sidrón assemblage. These results are in congruence with those from previous studies, which conclude that subvertical grooves are a common trait of Neandertal teeth (Villa and Giacobini, 1995; Poisson et al., 2000, Egocheaga et al., 2004).

In an attempt to explain the presence of subvertical grooves on Neandertal posterior dentition, Villa and Giacobini (1995) proposed that the high masticatory force levels among the Neandertals promoted the formation of subvertical grooves. However, Anton (1994) and O'Connor et al. (2005) stated that Neandertal facial configurations could not have generated high bite forces without overloading their TMJ (temporomandibular joints). As both adults and adolescents present subvertical grooves, occlusal wear was not severe in this sample and the occlusal wear has been statistically demonstrated not to be a factor conditioning the

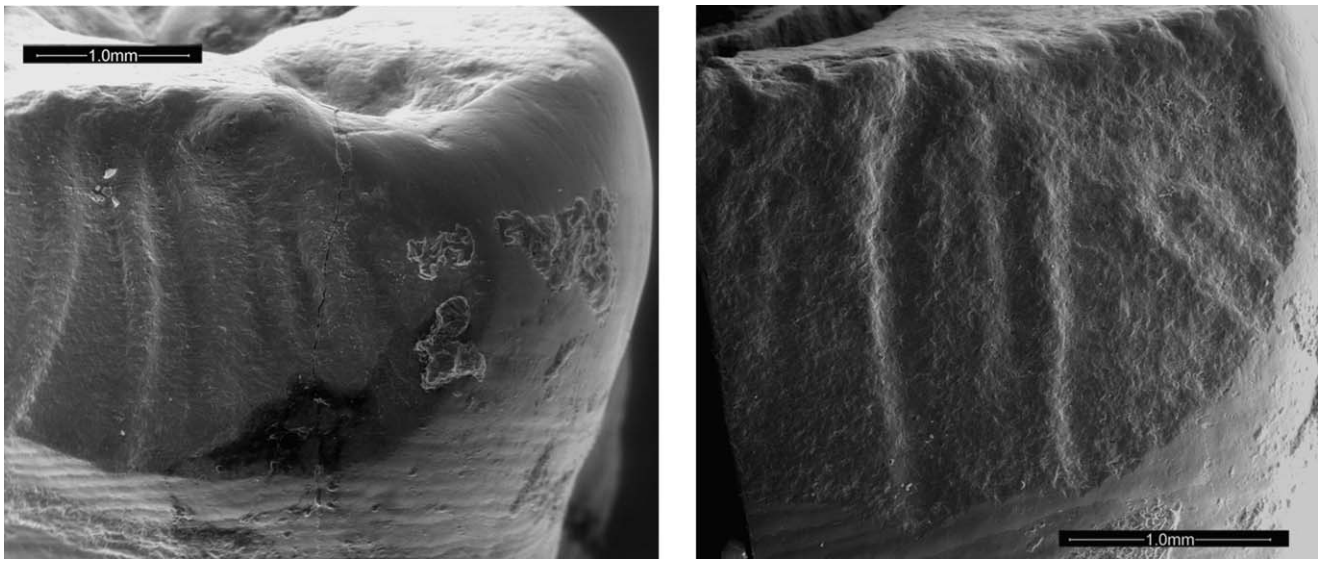

Fig. 3. Subvertical grooves on premolars from the El Sidrón sample. Right: Distal interproximal wear facet of a left lower second premolar (SD-303, LP_4) with seven deep and well defined subvertical grooves. Left: Distal interproximal wear facet of a left lower second premolar (SD-664, LP_4) with seven shallow but well-defined subvertical grooves.

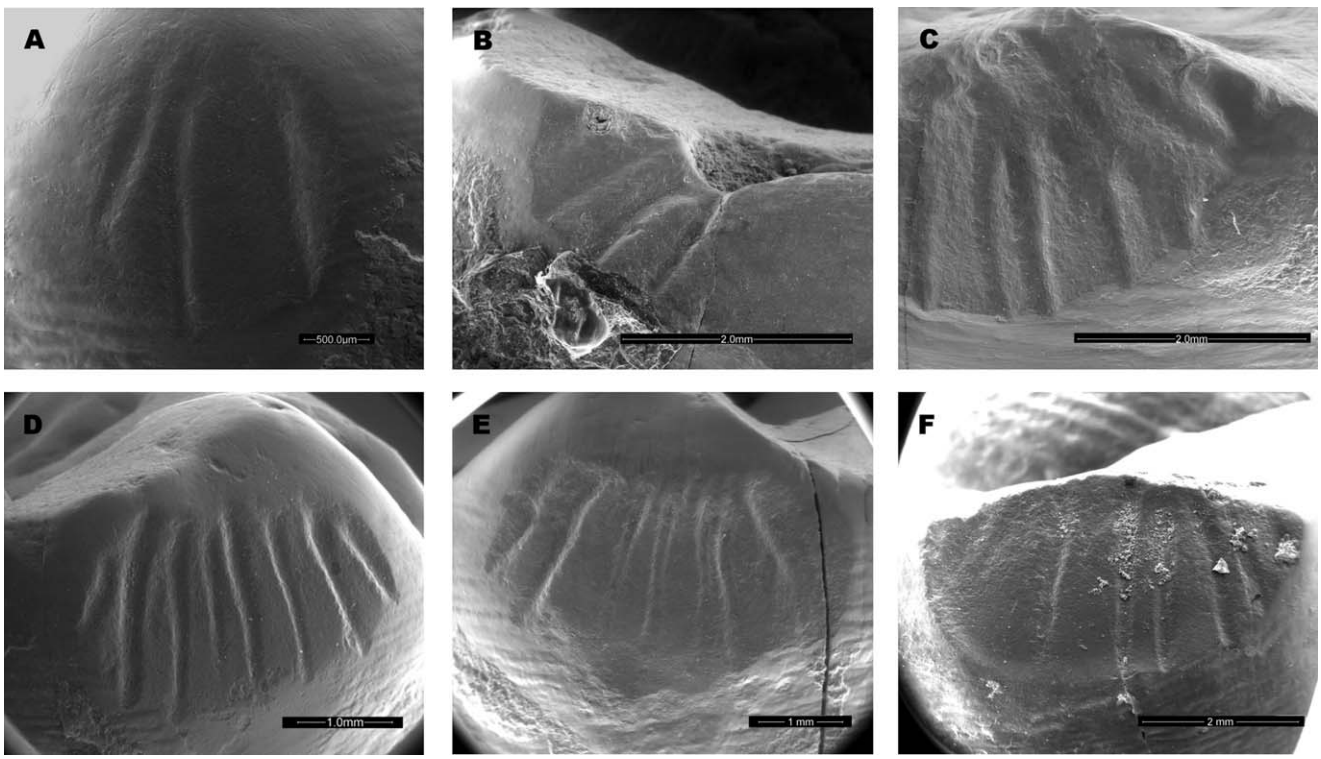

Fig. 4. Subvertical grooves on molars from the El Sidrón sample. **A:** Distal facet on SD-1327i (LM_2), with three straight subvertical grooves; **B:** Partial view of the mesial facet of SD-1218a (LM_2), with four subvertical grooves; **C:** Partial view of the distal facet of SD-1216c (RM_1) with seven subvertical grooves. Note that some grooves do not reach the cervical border of the facet; **D:** Distal interproximal wear facet of SDR-015 (RM_1) with eight deep and well-defined subvertical grooves. **E:** Distal facet of SD-756 (LM_1), with seven subvertical grooves with a zigzag shape in some of them; **F:** Distal facet of SD-1577 (LM_1) with eight subvertical grooves.

number and presence of subvertical grooves, these could be a product of the high masticatory forces rather than repetitive loading. Nevertheless, no microcracks were found in the El Sidrón sample nor TMJ degenerative joint disease, so high bite forces were not involved on the grooves formation. Thus, other factors (i.e., dietary habits, paramasticatory uses, enamel microstructure) seem to be involved.

The highest number of grooves per facet has been found on the P_4s, M_1s, and M_2s, whose interproximal facets are the widest of the dental arch. The statistical analyses show that the size of the facet is a factor affecting the number of grooves, but not highly significant, because it does not predict perfectly the number of subvertical grooves. Second premolars and first and second molars are responsible for the trituration of food during the chewing cycle, and they wear down quickly in hunter-gatherer populations (Molnar and Ward, 1977; Koolstra, 2002; Lucas, 2004; among others).

Neandertals are known to display a high rate of wear on the incisors (Smith, 1976; Brace, 1979; Ungar et al., 1997) ascribable to the use of their anterior teeth in both para-masticatory (de Lumley, 1973; Bermúdez de Castro et al., 1989; Lalueza-Fox and Frayer, 1997) and masticatory activities. Because the statistical analyses did not reveal a relation between the incisal wear and the number of grooves, it is probable that the use of anterior dentition in para-masticatory activities did not have any influence. This hypothesis must be further tested.

TABLE 2. Measurement mean for the width (occlusal end, medial, and cervical end), length and depth (in mm) of the subvertical grooves located in different tooth type and occlusal wear degree from the El Sidrón sample

Tooth class	Occl. wear	Width occ.	Width med.	Width cerv.	Depth	Length
Incisor	3	0.24	0.24	0.20	0.08	2.68
	4	0.33	0.26	0.19	0.09	1.95
Canine	5	0.31	0.32	0.35	0.12	1.73
	6	0.16	0.21	0.17	0.10	1.42
Premolar	2	0.10	0.10	0.11	0.07	0.91
	4	0.26	0.24	0.22	0.13	1.74
	5	0.22	0.24	0.21		1.47
Molar	2	0.32	0.29	0.22	0.22	1.32
	5	0.16	0.19	0.16	0.09	1.04
	6	0.26	0.28	0.28	0.13	1.49

Similarity in structure of subvertical grooves in the El Sidrón and other Neandertal samples (Kaidonis et al., 1992; Villa and Giacobini, 1995; Poisson et al., 2002; Pérez-Pérez et al., 2003) implies common functional etiology.

While Poisson et al. (2002) argued that mechanical abrasion was the cause of microcrack enlargement, Villa and Giacobini (1995) proposed chemical erosion as the most important factor involved in groove development due to the pitted surface at the bottom. We observed no differences between the surface of the bottom of the grooves and the surface of the interproximal wear facets (see Fig. 5). As tooth-to-tooth forces cause the interproximal facets, we suggest that subvertical grooves may be caused primarily by mechanical attrition.

Previous authors (Kaidonis et al. 1992) have stated that subvertical grooves "interdigitate" with each other when viewed from the occlusal plane. By contrast, we observed, as did Villa and Giacobini (1995) and Poisson et al. (2002), that subvertical grooves from adjacent facets display a mirrored distribution, instead of interdigitating. Our results suggest that a solid exogenous factor (e.g., food remains, sedimentary or bone particles) may have worked into the interproximal space to make the grooves, although no microwear was found on the groove surface. This situation could be analogous to the observations of Pérez-Pérez et al. (2003) that buccal microwear primarily reflects environmental conditions and dietary grit.

The deepest grooves appear on molars and premolars with slight occlusal wear, and that shallow grooves are more frequent on teeth with a moderate occlusal wear (Table 2), indicating that subvertical grooves formation begin soon after tooth eruption, and probably were eroded as interproximal attrition advances.

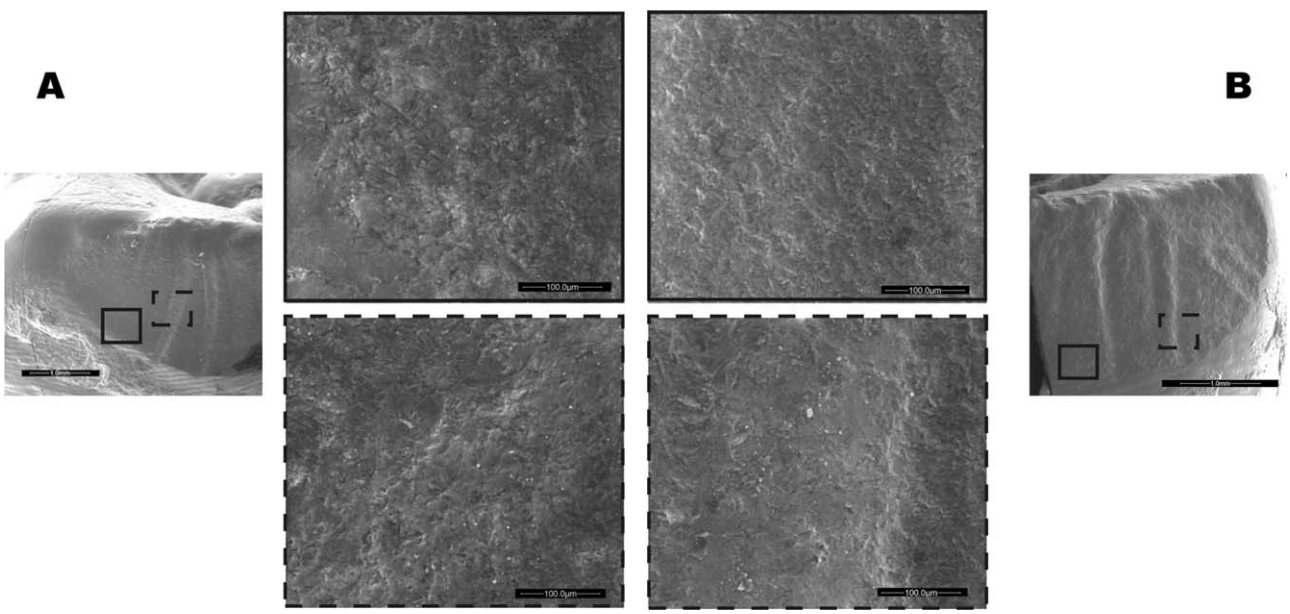

Fig. 5. Environmental scanning electron microscope (ESEM) micrograph at ×600 of the surface relief on the interproximal wear facet (upper), and the bottom of the groove (lower). No differences are observable between the surfaces. **A:** SD-664 LP_4, and **B:** SD-303 LP_4.

TABLE 3. General Linear Models (GLM) tests between the number of grooves and their position on the mesial and distal facets, the occlusal dental wear degree, facet width, and individual age estimation

	Effect	SS	Degr. of	MS	*F*	*P*
Occl. Wear	Fixed	0.572	1	0.572	0.165	0.685
Facet Width (mm)	Fixed	154.693	1	154.693	44.652	0.001
Position	Fixed	0.245	1	0.245	0.121	0.730
Age	Fixed		0			
Individual	Random	73.067	8	9.133	5.983	0.002
Error		342.975	99	3.464		

CONCLUSIONS

In this article we document the subvertical grooves on a new Neandertal sample from the El Sidrón cave (Asturias, Spain). When present, they are distributed on both the anterior and posterior dentition. The deepest grooves are on teeth with slight occlusal wear (in this sample in adolescents), which indicates that subvertical grooves were completely developed before the end of the biological maturation. Facet width is affecting the number of subvertical grooves, and the degree of occlusal wear is not associated with subvertical grooves formation. Subvertical grooves form small channels or mirroring grooves on adjacent facets, suggesting that could be formed due to erosion of dust particles taken with the diet. Neither a high masticatory forces nor a repetitive loading seem to be involved on the groove formation. Further analyses are needed in order to determine the contribution of these aspects to the origin of the subvertical grooves.

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CAPÍTULO V - LA LATERALIDAD MANUAL EN UN GRUPO NEANDERTAL Y SALUD BUCODENTAL

Los resultados de este estudio han sido publicados en las revistas:

Estalrrich, A., Rosas, A., 2013. Handedness in Neandertals from the El Sidrón (Asturias, Spain): Evidence from Instrumental Striations with Ontogenetic Inferences. PLoS One, 8(5): e62797.

Dean, M.C., Rosas, A., Estalrrich, A., García-Tabernero, A., Huguet, R., Lalueza-Fox, C., Bastir, M., de la Rasilla, M., 2013. Longstanding dental pathology in Neandertals from El Sidrón (Asturias, Spain) with a probable familial basis. Journal of Human Evolution, 64(6):678-86.

La lateralidad manual es la preferencia en el uso de la mano derecha o la izquierda cuando se desarrolla una actividad. En las poblaciones humanas actuales, la proporción diestros frente a zurdos es 9:1, definiendo a *Homo sapiens* como una especie eminentemente diestra en comparación con el resto de primates superiores (Hardyck *et al*., 1975; Perelle y Ehrman, 1994; Corballis, 2003; Cashmore *et al*., 2008; McManus, 2009; Frayer *et al*., 2012), es por eso que se piensa que este patrón de lateralidad manual se ha debido desarrollar únicamente en el linaje *Homo*. Cuando y en qué modo se produjo este desarrollo a nivel poblacional, es un tema que actualmente se está estudiando mediante el

análisis de la producción de herramientas líticas (Ollé, 2003; Steele y Uomini, 2005; Bargalló y Mosquera, 2013), el análisis de la orientación de las marcas de corte en los huesos (Shipman y Rose, 1983; Bromage y Boyde, 1984; Pickering y Hensley-Marschand, 2008), el estudio de la lateralidad cerebral en moldes endocraneales de homininos fósiles (Holloway *et al*., 2008), asimetrías en la morfología de los brazos (Trinkaus *et al*., 1994; Cashmore *et al*., 2008; Volpato *et al*., 2012), y la orientación de las estrías culturales (marcas producidas en la dentición anterior por el mismo individuo al cortar algún material que tenía sujeto con los dientes) en la cara labial de los incisivos y caninos (Bermúdez de Castro *et al*., 1988; Lalueza-Fox y Frayer,1997; Lozano *et al*., 2004, 2008; Frayer *et al*., 2010).

Los humanos del Pleistoceno medio usaban de manera preferente la mano derecha (Ollé, 2003; Bermúdez de Castro *et al*., 1988; Lozano *et al*., 2004, 2008, 2009; Frayer *et al*., 2012), mientras que en *Homo neanderthalensis* es de 93% diestros y 7% zurdos (Uomini, 2011), mostrando un patrón semejante al actual (Faurie *et al*., 2005).

Todos estos estudios se han llevado a cabo en individuos adultos. En esta tesis se ha planteado estudiar la lateralidad manual en *Homo neanderthalensis* con el propósito de conocer tanto si la lateralidad manual se manifiesta igual entre individuos adultos e inmaduros, y si la edad a la que la lateralidad manual se establece es la misma que en el hombre actual. Para ello se ha analizado la orientación de las estrías culturales en los 11 individuos Neandertales identificados en la cueva de El Sidrón que tienen dentición asociada, que, como se ha explicado en el capítulo anterior, son 7 adultos, 3 adolescentes y 1 juvenil.

Por otro lado, durante la caracterización de los individuos se ha observado que dos individuos presentan la retención de un canino de leche (El Sidrón Adulto 2 y El Sidrón Adolescente 3), y ambos tienen el mismo ADN-mt (Lalueza-Fox *et al*., 2011), lo que puede estar indicando una base genética y por tanto heredable en esta anomalía. Se ha decidido estudiar la posibilidad de que tuvieran alguna patología dental asociada y si esta patología tuviera algún efecto en la lateralidad manual de los individuos.

V.1 Metodología

Del estudio del desgaste dental se sabe que los Neandertales sujetaban un material con los dientes y una mano, y con la otra mano lo cortaban (Brace, 1975), arañando accidentalmente la superficie labial de sus dientes. Esos arañazos son unas estrías que tienen la misma morfología que las marcas de corte producidas en los huesos, de las que se puede saber la dirección y orientación con que se hicieron y por tanto inferir directamente la lateralidad manual del mismo individuo que las posee (Bermúdez de Castro *et al*., 1988; Lalueza-Fox y Frayer, 1997; Lozano *et al*., 2004, 2008; Frayer *et al*., 2010; Volpato *et al*., 2012).

Según los estudios experimentales y las evidencias estudiadas en diversos fósiles (Bermúdez de Castro *et al*., 1988; Lalueza-Fox y Frayer, 1997; Lozano *et al*., 2004), la orientación predominante en individuos diestros es la oblicua hacia la derecha (inclinación respecto al plano oclusal de 112,5º a 157,5º), mientras

que en individuos zurdos es la oblicua hacia la izquierda (inclinación respecto al plano oclusal de 22,5º a 67,5º).

En esta tesis se ha estudiado la orientación de las estrías culturales en 66 incisivos y caninos asignados a los individuos mencionados. Los dientes se han examinado directamente en el MEB de cámara ambiental (ESEM Fei-Quanta 200®). Como 21 dientes se encuentran *in situ*, ha habido que realizar moldes de alta resolución, siguiendo el mismo procedimiento explicado en el capítulo anterior. La orientación de la estrías respecto al plano oclusal se ha medido directamente en las imágenes digitales obtenidas mediante el programa Image J (Rasband, 2006).

Para saber si las estrías siguen una orientación predominante o bien están distribuidas al azar y por tanto no se puede inferir lateralidad manual, se ha realizado un test X^2 o Chi-cuadrado ($p< 0,05$).

Para el análisis de los caninos de leche y su posible patología, se han realizado radiografías y escáneres CT médicos (con una anchura de corte de 0,625 mm, y una resolución de 0,344 mm).

V.2 Resultados

Todos los individuos estudiados presentan estrías culturales. La orientación predominante en la muestra es oblicua hacia la derecha (58% del total de las estrías analizadas), seguida de una orientación horizontal (17%), vertical (15%) y por último oblicua hacia la izquierda (11%).

El diente que mayor número de estrías posee es un incisivo lateral maxilar del individuo Adolescente 2 con 39 estrías. Los individuos Adulto 1, Adulto 3 y Adulto 4 le siguen en número con 32, 31 y 31 estrías respectivamente.

El valor del estadístico Chi-cuadrado es de 7,815, con una significación de 0,000001, indicando que las estrías se distribuyen siguiendo una orientación preferente.

El patrón de orientación predominante de las estrías culturales en los Neandertales de El Sidrón es oblicuo hacia la derecha, indicando que todos son individuos diestros. Estos resultados incluyen al individuo Juvenil 1, con una edad estimada de 7,5 años, que presenta varias estrías culturales con morfología similar a la de los individuos adultos, aunque las estrías son ligeramente curvadas, algo más cortas y menos numerosas.

Los escáneres y radiografías han mostrado que mientras El Sidrón Adolescente 3 no muestra ninguna patología asociada, El Sidrón Adulto 2 presenta un quiste en la raíz de LLM1. Este individuo además presenta casi el mismo número de estrías oblicuas hacia la derecha (n=53) que hacia la izquierda (n=44). Aunque el número de estrías características de diestros son un poco más numerosas, las estrías orientadas hacia la izquierda aparecen cubriendo a las demás, y con un aspecto más reciente.

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Handedness in Neandertals from the El Sidrón (Asturias, Spain): Evidence from Instrumental Striations with Ontogenetic Inferences

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Abstract

The developed cognitive capabilities for *Homo sapiens* seems to be the result of a specialized and lateralized brain, and as a result of this, humans display the highest degree of manual specialization or handedness among the primates. Studies regarding its emergence and distribution within the genus *Homo* show that handedness is present very early. The mode in which it was articulated and spread across the different species during the course of human evolution could provide information about our own cognitive capacities. Here we report the manual laterality attributed to eleven 49,000 old Neandertal individuals from El Sidrón cave (Spain), through the study of instrumental or cultural striations on the anterior dentition. Our results show a predominant pattern addressed to right-handers. These results fit within the modern human handedness distribution pattern and provide indirect evidence for behavior and brain lateralization on Neandertals. They support the early establishment of handedness in our genus. Moreover, the individual identified as Juvenile 1 (6–8 years old at death), displays the same striation pattern as the adult Neandertals from the sample, and thereby the ontogenic development of manual laterality in that Neandertal population seems to be similar to that of living modern humans.

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Introduction

Handedness is the tendency to display left- or right-hand task preference, and modern humans show a high frequency of right hand specialization compared to all great apes, meaning that such pattern of manual laterality should have been developed only in our actual lineage.

In order to understand and define how and when handedness evolved at population-level, several studies have been carried out through the paleoanthropological record employing different methodologies like stone tool production [1;2;3], the analysis of cut mark orientation on bones [4;5], brain lateralization from endocasts [6], asymmetries in hominid upper limb skeletons [7], and the orientation of scratches striating the labial surface of anterior teeth [8].

As a result it is acknowledged that during Middle Pleistocene, *Homo heidelbergensis* had an exclusively right-handed preference [1;8;9;10;11;12].

For Neandertals, widespread evidence from France to Spain to Croatia, beginning at least 130,000 years ago shows that they followed a right-handed pattern close to that characteristic to modern *Homo sapiens*. Studies by Bermúdez de Castro *et al.* [8], Trinkaus *et al.* [13], Lalueza-Fox and Frayer [14], Frayer *et al.* [15] and Volpato *et al.* [16] on skeletal evidence, indicate that although there is a predominant right-hand use at species-level, at least two individuals with a left-handed preference have been identified, showing a frequency of 93% right-handers to 7% left-handers [16]. Thus, Neandertals show a frequency identical to modern human populations [17;18].

This study analyzes the directionality of the instrumental or cultural striations present on the anterior teeth of eleven individuals of known sex and age from El Sidrón cave (Asturias, Spain), substantially increasing the Neandertal sample.

El Sidrón Cave

The sample comprises teeth from the Neandertal fossils of El Sidrón cave, which are housed at the Department of Paleobiology at National Museum of Natural History (MNCN- CSIC) in Madrid, Spain. The age of the bone assemblage has been estimated at ~49 kya [19;20]. At the moment, the minimum number of individuals (MNI) identified at the site is 13, including seven adults, three adolescents, two juveniles and one infant [21;22]. We have genetic profiles for each individual, so we are reasonably certain of the sex, based on presence (or absence) of Y chromosome markers [21]. So, unlike other studies which estimates sex based on size or robusticity, we approached the sex-estimation also from paleogenetics. The combined results show that the sample comprises at least 3 adult females, 3 adult males, 2 adolescent males, and 1 juvenile possible male. For 4 individuals it was not possible to retrieve genetic material and the skeletal evidence was not enough to fairly conclude the estimation. In

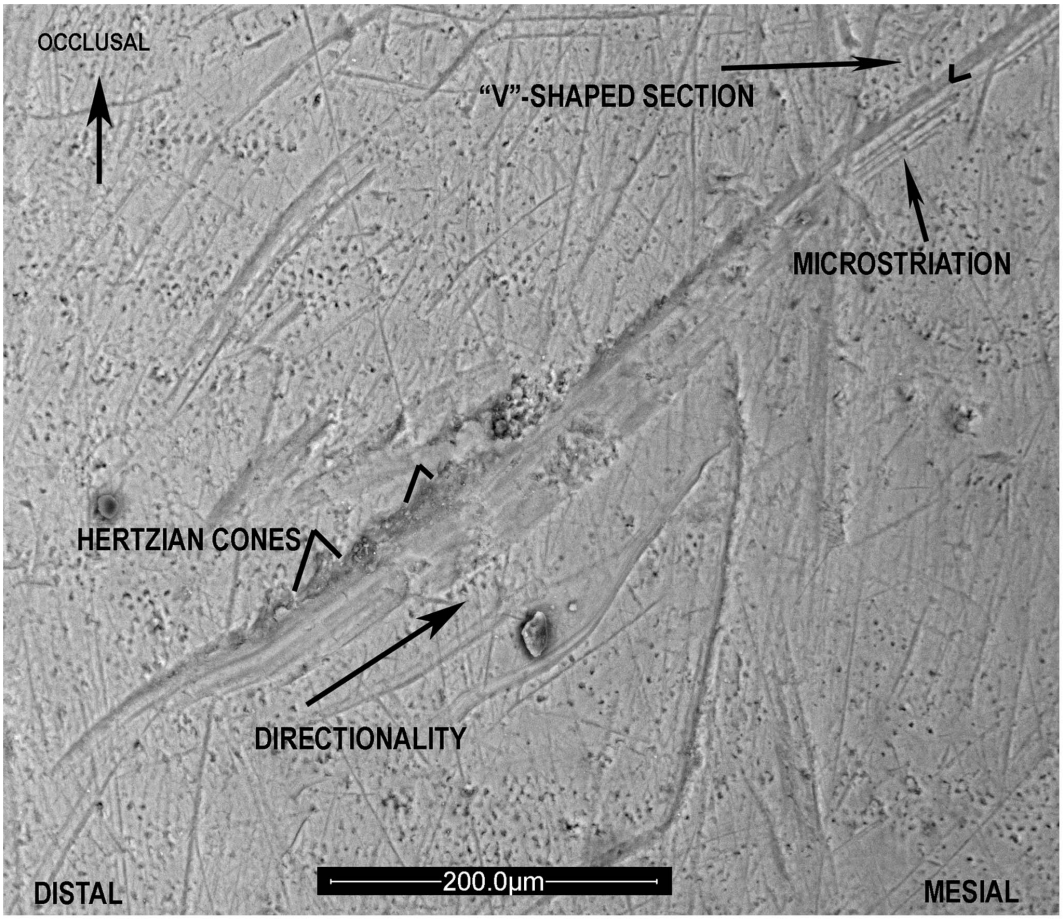

Figure 1. Cultural or Instrumental striation morphology. 200× picture of SD-355 (RI_2) associated to individual Adult 4. Cut mark features are indicated on the image. Directionality is from cervix to the incisal edge.
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addition, several human remains show evidence that they were subject to cannibalism [22;23].

The dental fossil sample selected for this study comprises 66 teeth (62 are permanent teeth while 4 are deciduous teeth) corresponding to 11 of the 13 individuals identified at the El Sidrón cave. A complete list of the specimens here analyzed with their catalogue number, anatomical identification and individuals assignment is provided on supplementary materials (Table S1). The individuals infant 1 and juvenile 2 do not have associated teeth. No taphonomical, excavation or preparation damage have been observed on the teeth [22;23]. All dental modifications observed on teeth are clearly related to both masticatory and non-mastication wear (see Figure 1 as an example of the good preservation of dental surface). Posterior teeth show no evidence of buccal (or labial) striations.

Instrumental or Cultural Striations

Instrumental or cultural striations are cut marks associated with the use of teeth as a third hand, known as the "stuff-and-cut" behavior [24]. Brace [24] used this term to describe differential, heavy wear on Neandertal incisors and canines compared to their premolars and molars. When an individual holds some material between the teeth with one hand pulling and the opposite hand cutting the material, scratches are sometimes left on the labial surface of incisors and canines when the lithic tool accidentally glances the tooth surface. Experimental work using teeth from dental extractions [8;9] has produced cut marks on enamel similar to those found on original Neandertal teeth.

Several authors have characterized the morphology of cultural striations on Pleistocene hominids ([8;9;10;11;14;15;16], among others). The scratches appear mostly on the labial surface of the central and lateral incisors and are more common in the central area than the mesial or distal sides of the teeth. On the canine they most commonly occur near the mesial surface. Their length varies between 1 to 4 mm and the width varies from 20 to 100 microns. These striations exhibit the same morphological features of the cut marks on bone [4;25;26], *i.e.*, Hertzian cones, grooves with a "V"-shaped section, and microscratches at the bottom, which vary depending on the stone tool that produced the striation [9], and, at least, linear and parallel borders. Because of this morphology it is possible to establish the directionality of the cut mark [26] and infer the manual laterality of the individual who has made the cut mark.

Based on these features, Bermúdez de Castro *et al.* [8], Lalueza-Fox and Frayer, [14] and Lozano-Ruíz *et al.* [9], linked the orientation and directionality of the cultural striation with a preferred hand movement, leading to the establishment of a direct relation between the individual's hand movement and the directionality of the cultural striation. Once a statistical significance was reached, it allowed the assignment of handedness to individuals.

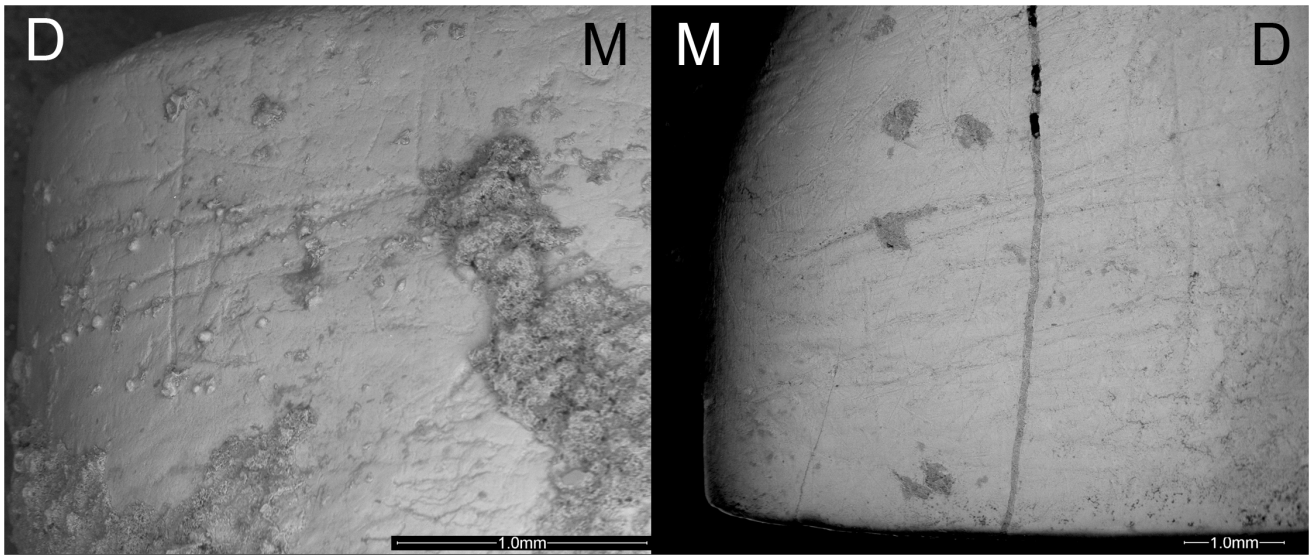

Figure 2. Instrumental striations present on the El Sidrón Adolescents. Left: LI_2 from Adolescent 1. Right: LI^1 belonging to Adolescent 2. All instrumental striations are distinguishable, and some are also still slightly covered by sediment, that reinforces their ancient origin. M = mesial; D = distal.
doi:10.1371/journal.pone.0062797.g002

Instrumental striations have been reported on Middle and Late Pleistocene fossil hominids from the sites of La Quina [27;28], L'Hortus [29;8], Cova Negra [8], Shanidar [30], Krapina [14], Vindija [15], Regourdou [16], Tabun I [28], Broken Hill [28], Boxgrove [31] and Sima de los Huesos [8;9;10;12], as well as in several modern human populations, such as the Chalcolithic individuals from Pakistan [32], Neolithic from Spain [33] and Sweden [34], Paleoindian from North America [35], Australian Aborigines [10], and Fueguians [33].

Methods

Each tooth was inspected under binocular lens and Environmental Scanning Electron Microscope (ESEM Fei- Quanta 200 © located in the National Museum of Natural History (MNCN-CSIC). All teeth were examined at 25.0 kv accelerating voltage and low vacuum mode. The magnification observations ranged from 40× to 1000× in some instances.

As 21 teeth were found *in situ* (in their respective *alveoli* on both the maxilla and mandible), it has been necessary to perform high-resolution replicas of them, due to the limited dimensions of the microscope's chamber. Following the procedures described elsewhere in detail, a hydrophilic vinyl polysiloxane resin was employed to make the negative cast [26], and a polyurethane resin to make the replica [36]. Using a low viscosity variety it is possible to produce replicas of great resolution and the details on the negative impression can last more than a year; polyurethane has a moderately fast drying time, excellent viscosity and fluidity that allow faithfully details reproduction of the enamel surface. Finally,

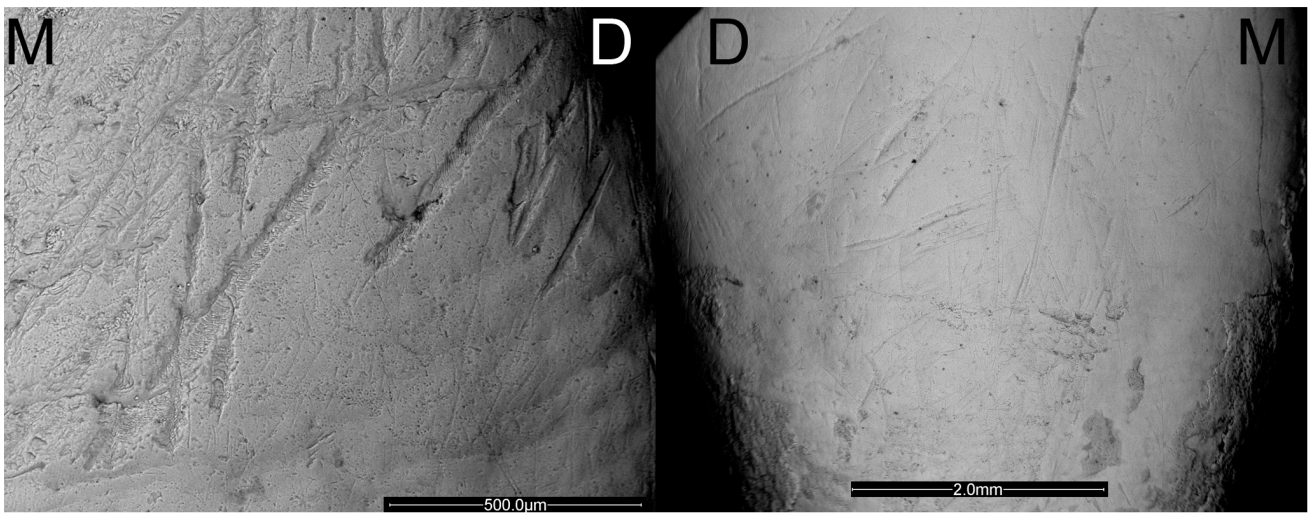

Figure 3. Instrumental striations present on two El Sidrón Adult females. Scanning Electron Microscope images of the instrumental striations identified on the left upper canine on Adult 3 (Left) and on the right lower lateral incisor from Adult 4 (Right). M = mesial; D = distal.
doi:10.1371/journal.pone.0062797.g003

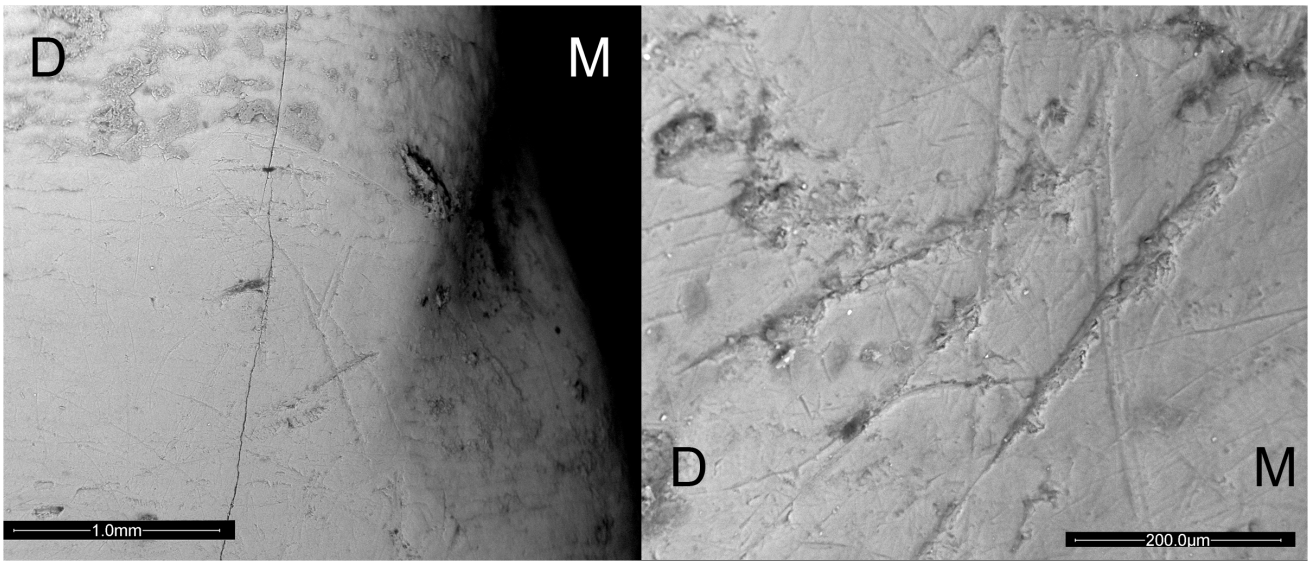

Figure 4. Instrumental striations present on one El Sidrón Adult males. ESEM micrographs of the labial surface of the upper right central incisor and upper right canine belonging to Adult 1. M = mesial; D = distal.
doi:10.1371/journal.pone.0062797.g004

the replicas were covered with a thin layer of metallic gold (Sputter Coater, EMITECH K550Y®) to allow the ESEM visualization.

The orientation of the *striae* to the occlusal plane was measured directly on digital images (NIH Image J, Image Processing and Analysis in Java; [37]). In this study, we have considered the instrumental striations that have an undoubted cut-mark morphology, that is: we did not count the scratches that appear worn (cut-mark morphology is almost removed, and thus we cannot be sure about their origin) or the ones that are short and thin (thinner than 20 microns and length less than 1 mm, as was described before according to the results on the Krapina Neandertals sample [14]), and could be confused with dietary dental microwear. Orientation's classification was made following Bermúdez de Castro *et al.* [8]. X^2 tests were performed to examine the significance ($p<0.05$) of the striations' distribution on each individual.

Results

All individuals studied at the El Sidrón site present instrumental striations (Figures 2, 3 and 4). The results of the characterization of the orientation for each tooth associated to an individual are shown in Tables 1 and 2. Considering them as a group, the preferred orientation is right-oblique (58% of the total number of cultural striations analyzed), followed by the horizontal orientation (17% of the total). Vertical (14%) and left-oblique (11%) orientations are also present in all the individuals but their frequencies are not high.

The tooth with the highest number of cultural striations registered in the sample belongs to adolescent 2, followed by adult 1 and adults 3 and 4. Regarding the strations' measurements on the sample, the mean length is 2.063 mm (SD = 0.147) and the mean width is 43.5 microns (SD = 16 microns), similar to the Krapina Neandertals [14].

Juvenile 1 has several instrumental striations, whose morphology has been carefully studied, and coincide with the cultural striations pattern, like the adult Neandertals from the sample, as shown in Figure 5.

The X^2 analyses comparing the number of right vs left scratches reveal that all X^2 values exceed the table value of 7.815 (at 3 degrees of freedom and $p<0.00001$). Based on this we can reject the null hypothesis of a random distribution in favor of the hypothesis the striations are showing a preferred orientation on every El Sidrón Neandertal (Table 3), which is right-oblique.

Discussion

As said, all individuals analyzed from the El Sidrón individuals have cut marks on their erupted anterior dentition. Our results show a predominantly right-oblique orientation of the instrumental striations, typically ascribed to right-handers [14]. The results match with the modern human handedness pattern, and provide additional indirect evidence for Neandertal brain lateralization. This handedness pattern, together with the asymmetries on cranial dural sinuses and blood drainage [38], the morphology of hyoid bone [39] and the same derived FOXP2 variant of modern humans [40] as part of the basis for human speech capability, reinforces a modern brain asymmetry pattern in Neandertals.

In our sample we found a substantial number of vertical striations (177 out of 1233, or 14% of the total striations counted). The vertical marks have been associated with the processing of plant fibers in Paleoindian populations [41] and according to the authors, it is not possible to address a manual preference on the sample they studied. Since the marks described by Bax and Ungar [41] display the characteristic cut mark morphology associated to the instrumental striations here considered, and are also shorter and thinner, we consider that the behavior responsible for the scratch formation is different in both samples. Therefore, it is not recommended to analyze all the anterior scratches to address handedness in past populations.

Individual adult 2 presents almost the same number of right and left-oblique striae, but the left ones are covering the right oriented striations. This pattern appears on both mandibular and maxillary dentition, but is more evident on the lower teeth (Fig. 6). Despite this, the interpretation of X^2 results show that this individual is right-handed. The presence of a severe oral pathology on the left side on his mandible [42] plus dental calculus deposits on the

Table 1. Instrumental striations on the El Sidrón adult Neandertals.

	MAXILLARY DENTITION						MANDIBULAR DENTITION					
INDIVIDUAL	**RC**	**RI2**	**RI1**	**LI1**	**LI2**	**LC**	**RC**	**RI2**	**RI1**	**LI1**	**LI2**	**LC**
ADULT 1	n = 32	n = 19	n = 24	n = 16	n = 20	n = 16	n = 17	n = 13	n = 14		n = 13	n = 15
	RO = 19	RO = 10	RO = 15	RO = 9	RO = 11	RO = 12	RO = 11	RO = 8	RO = 12		RO = 6	RO = 9
	H = 4	H = 3	H = 2	H = 3	H = 3	H = 0	H = 1	H = 2	H = 1		H = 4	H = 4
	LO = 3	LO = 2	LO = 3	LO = 1	LO = 3	LO = 2	LO = 2	LO = 0	LO = 0		LO = 1	LO = 1
	V = 6	V = 4	V = 4	V = 3	V = 3	V = 2	V = 3	V = 3	V = 1		V = 2	V = 1
ADULT 2	n = 8	n = 14	n = 15	n = 17	n = 12	n = 16	none	n = 16	n = 16	n = 17	none	none
	RO = 3	RO = 5	RO = 6	RO = 9	RO = 4	RO = 6		RO = 6	RO = 7	RO = 7		
	H = 2	H = 1	H = 0	H = 2	H = 3	H = 2		H = 5	H = 2	H = 4		
	LO = 3	LO = 7	LO = 7	LO = 4	LO = 3	LO = 7		LO = 4	LO = 4	LO = 5		
	V = 0	V = 1	V = 2	V = 2	V = 2	V = 1		V = 1	V = 3	V = 1		
ADULT 3	none	none	none	none	none	n = 31	none	n = 17	n = 12	none	none	none
						RO = 23		RO = 8	RO = 8			
						H = 4		H = 3	H = 3			
						LO = 3		LO = 2	LO = 1			
						V = 1		V = 4	V = 0			
ADULT 4	n = 15	none	none	n = 31	none	n = 26	n = 23	n = 27	n = 29	n = 29	n = 18	none
	RO = 8			RO = 19		RO = 15	RO = 17	RO = 14	RO = 21	RO = 23	RO = 13	
	H = 2			H = 5		H = 4	H = 3	H = 6	H = 4	H = 4	H = 4	
	LO = 1			LO = 2		LO = 2	LO = 0	LO = 4	LO = 3	LO = 0	LO = 0	
	V = 4			V = 5		V = 5	V = 3	V = 3	V = 1	V = 2	V = 1	
ADULT 5	n = 8	n = 18	n = 17	n = 25	n = 22	n = 8	none	n = 15	n = 26	n = 22	n = 22	n = 16
	RO = 7	RO = 11	RO = 11	RO = 17	RO = 13	RO = 5		RO = 7	RO = 23	RO = 9	RO = 13	RO = 7
	H = 0	H = 2	H = 2	H = 3	H = 4	H = 2		H = 3	H = 0	H = 6	H = 6	H = 5
	LO = 0	LO = 2	LO = 0	LO = 2	LO = 3	LO = 0		LO = 1	LO = 1	LO = 2	LO = 1	LO = 1
	V = 1	V = 3	V = 4	V = 3	V = 2	V = 1		V = 4	V = 2	V = 5	V = 2	V = 3
ADULT 6	none	none	none	n = 18	none	n = 22	none	none	none	none	n = 21	n = 26
				RO = 11		RO = 15					RO = 8	RO = 11
				H = 3		H = 4					H = 8	H = 9
				LO = 3		LO = 1					LO = 2	LO = 1
				V = 1		V = 2					V = 3	V = 5
ADULT 7	none	n = 22	n = 20	none	none	none	none	none	none	none	none	none
		RO = 15	RO = 11									
		H = 3	H = 3									
		LO = 1	LO = 2									
		V = 3	V = 4									

In this table are the results for the analysis of the total number of instrumental striations counted per tooth (n) and the number of scratches depending on their orientation. RC: right canine; RI2: right lateral incisor; RI1: right central incisor; LI1: left central incisor; LI2: left lateral incisor; LC: left canine. RO: right-oblique orientation; LO: left-oblique orientation; V: vertical orientation; H: horizontal orientation; n:.

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occlusal molar surface, suggest that this individual may have changed his hand orientation to avoid the pain on his mouth, and can explain the fact that the left-oriented striations appear new when compared with the right ones. We propose that chewing with the left and even the action of holding materials for processing could be painful. That could have motivated the individual to start using the right side of his teeth to seize materials and later cut them, adapting his manual laterality to his actual circumstances. According to the well-preserved striae's morphology (Figure 6), this change may have happened fast, and since no postcranial elements have been associated to this individual yet, we propose the pathological condition as the most plausible explanation.

Juvenile 1 displays the same striation pattern as the other adult Neandertals from the sample, although the number of scratches is slightly below the adults. The number of scratches varies depending on how many times the individual have repeated the action [10]. So, despite the juvenile seems to have performed this task less often than adults, the number indicates that it could be an habitual behavior, and he left enough cut marks on his front teeth to describe him as a right-handed individual.

Table 2. Instrumental striations on the El Sidrón immature Neandertals.

	MAXILLARY DENTITION						MANDIBULAR DENTITION					
INDIVIDUAL	**RC**	**RI2**	**RI1**	**LI1**	**LI2**	**LC**	**RC**	**RI2**	**RI1**	**LI1**	**LI2**	**LC**
ADOLESCENT 1	n = 10	none	none	none	none	none	none	n = 13	n = 27	none	none	none
	RO = 7							RO = 6	RO = 16			
	H = 1							H = 2	H = 3			
	LO = 1							LO = 1	LO = 2			
	V = 1							V = 4	V = 6			
ADOLESCENT 2	none	n = 39	n = 28	n = 24	none	none	none	n = 16	none	none	none	none
		RO = 27	RO = 18	RO = 12				RO = 9				
		H = 6	H = 3	H = 7				H = 3				
		LO = 2	LO = 3	LO = 3				LO = 4				
		V = 4	V = 4	V = 2				V = 0				
ADOLESCENT 3	none	none	none	n = 15	n = 15	n = 16	none	none	none	none	none	none
				RO = 7	RO = 9	RO = 14						
				H = 3	H = 0	H = 2						
				LO = 4	LO = 1	LO = 0						
				V = 1	V = 5	V = O						
JUVENILE 1	n = 6*	none	n = 16	n = 20	none	none	n = 14*	n = 18*	n = 16	n = 19	none	n = 7*
	RO = 4		RO = 4	RO = 7			RO = 8	RO = 9	RO = 12	RO = 9		RO = 3
	H = 1		H = 5	H = 4			H = 2	H = 2	H = 3	H = 2		H = 1
	LO = 0		LO = 2	LO = 3			LO = 1	LO = 0	LO = 1	LO = 3		LO = 2
	V = 1		V = 5	V = 6			V = 3	V = 7	V = 0	V = 5		V = 1

The results for the analysis of the number of instrumental striations (n) counted on each tooth and the number according to their orientation through the occlusal/incisal plane on the El Sidrón adolescent and juvenile Neandertals. * Indicate deciduous teeth. RC: right canine; RI2: right lateral incisor; RI1: right central incisor; LI1: left central incisor; LI2: left lateral incisor; LC: left canine. RO: right-oblique orientation; LO: left-oblique orientation; V: vertical orientation; H: horizontal orientation.
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Previous studies dealing with those scratches were done on adult Neandertals, so this is the first time that handedness has been found in a juvenile Neandertal. The estimated age for this individual is about 6–8 years old, so it seems that the ontogenic development of manual laterality in that Neandertal population is similar to that of actual modern humans. In this specie an

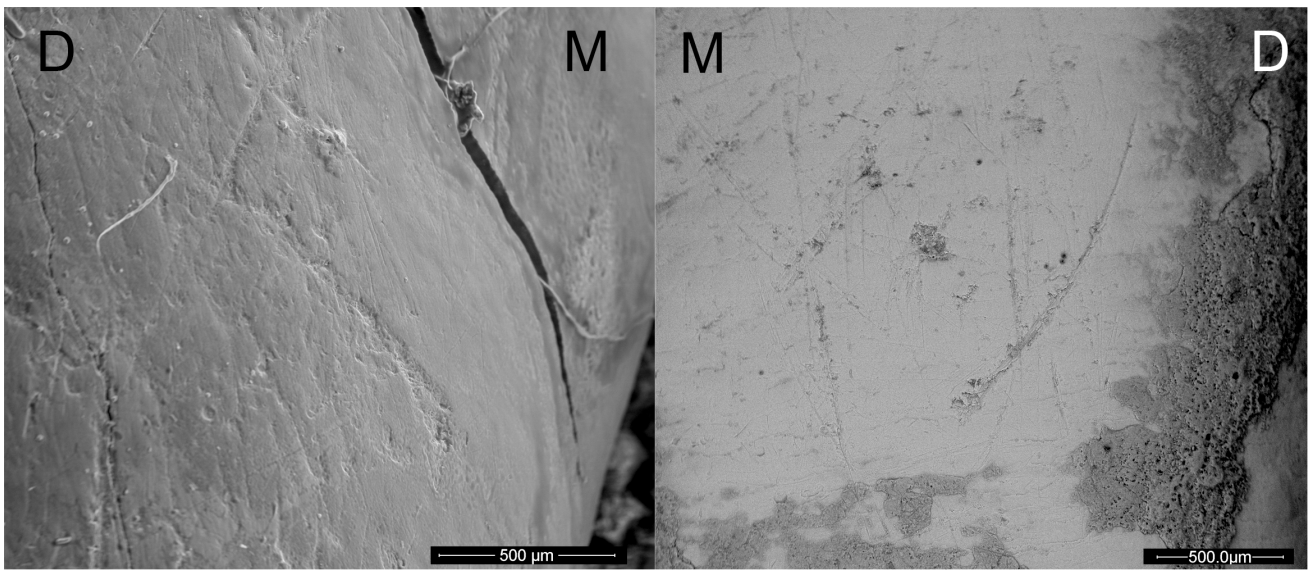

Figure 5. Instrumental striations on one El Sidrón Adult and the juvenile Neandertal. Morphological comparison between the instrumental striations found on: Left: a mandibular right deciduous lateral incisor (SD-1600c) from Juvenile 1; and Right: a mandibular right lateral incisor belonging to Adult 5 (SD-1327a). M = mesial; D = distal.
doi:10.1371/journal.pone.0062797.g005

Table 3. Comparison of number of right vs left scratches.

Individual	Chi-square	df	p
Adult 1	70.16	3	<.0000001
Adult 2	24.48	3	<.0000001
Adult 3	87.12	3	<.0000001
Adult 4	91.68	3	<.0000001
Adult 5	75.76	3	<.0000001
Adult 6	46.64	3	<.0000001
Adult 7	75.12	3	<.0000001
Adolescent 1	62.24	3	<.0000001
Adolescent 2	74.80	3	<.0000001
Adolescent 3	85.44	3	<.0000001
Juvenile 1	34.60	3	<.0000001

The results of the X^2 analysis (x^2 values exceed the table value of 7.815 at 3 degree of freedom) show that all values accept a preferred orientation regarding the instrumental striations' distribution, and in this sample is oblique to the right.
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unimanual hand use for reaching objects has been detected early on infants [43], although manual laterality preference when performing complex tasks and bimanual actions appear on later age [44] and it is completely established around seven years of age [45].

Bermúdez de *Castro et al.* [8] and Lozano *et al.* [10] presented results of handedness for subadult individuals (mostly adolescents) for the SH sample. On their results, they show evidence for right-handedness on adolescent individuals, and even on one individual with an estimated age at death of 3–4 years old. This individual has only 2 cut marks on one tooth, so we are not sure if it could indicate an incipient establishment of handedness or maybe its number is underrepresented because the individual's anterior dentition has not been recovered.

According to our results, the El Sidrón individuals are all right-handed, and when comparing to other Neandertals described in the literature, the distribution of manual laterality coincides with the handedness distribution at the Vindija cave and Atapuerca-Sima de los Huesos site, whose population appears to consist exclusively of right-handed individuals [9;10;12]. At the Neandertal sites of Hortus [29] and Krapina [14] the dominant trend is the same, oblique to the right, but two specimens (KDP 4 and Hortus VII) have an oblique to the left predominant orientation, which is characteristics of left-handed individuals. Table 4 summarizes the findings regarding manual lateralization in Neandertals by the study of cultural striations, including the last findings at the El Sidrón fossils. At population level in Neandertals, the distribution of handedness based on this feature is 27 right-handers to 2 left-handers, or 93% to 7% [16;18].

This is consistent with the distribution of manual dexterity in modern humans, which in any population, left-handed individuals are expected to be between 3% and 25% of the total, while right-handed individuals could be between 97% and 75% of the population [17]. This is a highly variable range, but indicates that the most probable manual laterality in one population is the right-handed one [17]. In our case, all individuals identified match with right-handed individuals, as was expected in a human population.

Regarding the behavioral consequences derived from the manual laterality, a recent model proposed by Abrams and Panaggio [46], states that the high prevalence of the same manual laterality pattern at the populational level, may suggest a

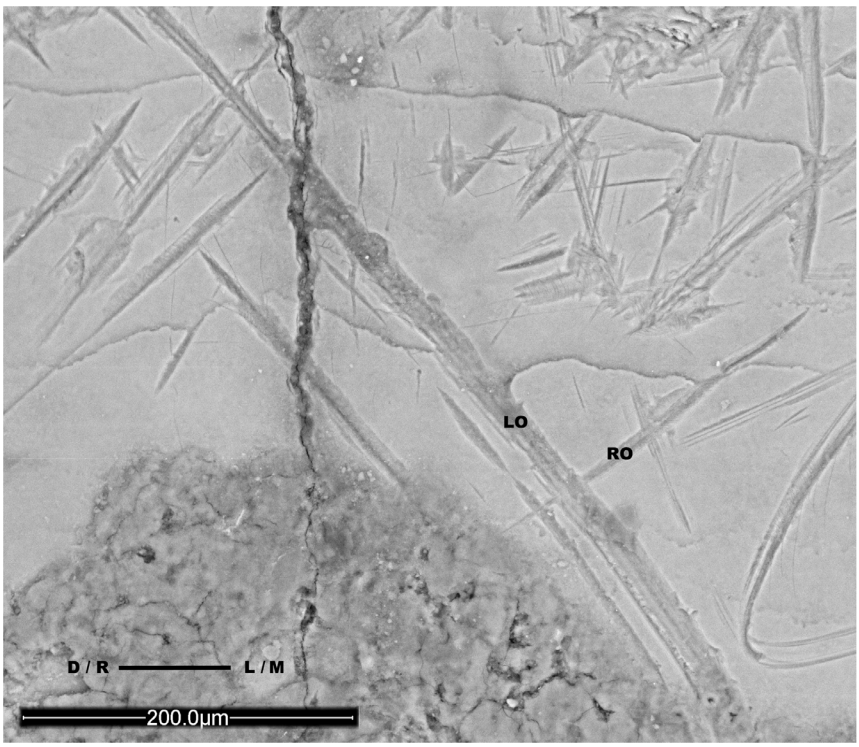

Figure 6. The peculiar case found on El Sidrón Adult 2. ESEM image showing the left-oblique striations covering the right-oblique on a RI_1 from Adult 2. M = mesial; D = distal. R = right; L = left.
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Table 4. List of Neanderthal sites where handedness has been identified from cultural striations.

INDIVIDUAL	HANDEDNESS	REFERENCES
Cova Negra	R	Bermúdez de Castro *et al.* 1988
Hortus VII	L	de Lumley, 1973; Bermúdez de Castro *et al.* 1988
Hortus VIII	R	de Lumley, 1973; Bermúdez de Castro *et al.* 1988
Hortus IX	R	de Lumley, 1973; Bermúdez de Castro *et al.* 1988
Hortus XI	R	de Lumley, 1973; Bermúdez de Castro *et al.* 1988
Hortus XII	R	de Lumley, 1973; Bermúdez de Castro *et al.* 1988
KDP 4	L	Lalueza-Fox & Frayer, 1997
KDP 5	R	Lalueza-Fox & Frayer, 1997
KDP 6	R	Lalueza-Fox & Frayer, 1997
KDP 17	R	Lalueza-Fox & Frayer, 1997
KDP 18	R	Lalueza-Fox & Frayer, 1997
KDP 29	R	Lalueza-Fox & Frayer, 1997
KDP Q	R	Lalueza-Fox & Frayer, 1997
Le Régourdou 1	R*	Volpato *et al.*, 2012
Vindija 206	R	Frayer *et al.*, 2010
Vindija 288	R	Frayer *et al.*, 2010
Vindija 289	R	Frayer *et al.*, 2010
Vindija 290	R	Frayer *et al.*, 2010
Sidrón Adult 1	R	This study
Sidrón Adult 2	R	This study
Sidrón Adult 3	R	This study
Sidrón Adult 4	R	This study
Sidrón Adult 5	R	This study
Sidrón Adult 6	R	This study
Sidrón Adult 7	R	This study
Sidrón Adolescent 1	R	This study
Sidrón Adolescent 2	R	This study
Sidrón Adolescent 3	R	This study
Sidrón Juvenile 1	R	This study

On the left column are the specimens that have been studied, and the references of the study (column on the right). The identification as a right- (R) or left-hander (L) is on the central column. KDP: Krapina Dental Person [47]. This table extends the data provided by Uomini [18], considering only data from the analysis of labial scratches.
* = data also from humeral morphology.
doi:10.1371/journal.pone.0062797.t004

collaborative society with low level of intra-society violence. This was the first model to make a clear correlation between population-level handedness and social behavior and, if we apply its conclusions to the extreme frequency of right-handedness in Neandertals it may suggest a cooperative society, or at least among groups such as the El Sidrón group.

Conclusions

Individuals identified from the El Sidrón dental sample present a predominant right-oblique orientation of their instrumental striations, typically related to right-handed individuals. The results enhance the knowledge of Neandertal manual laterality and provide additional indirect evidence for Neandertal brain lateralization.

One individual, identified as adult 2, presents evidence for a change in his manual motion, probably as a result to avoid pain on his unhealthy mouth. This could suggest a rapid adaptative behavior in this group.

The handedness' distribution in Neandertals and its ontogenetic development match within the modern human laterality pattern at population level, and may have behavioral and social applications to this fossil species. In addition, those results are giving information about the evolutionary development and establishment of our own asymmetric hand use, indicating that the achievement of this pattern may be shared with our common ancestor.

Supporting Information

Table S1 List of the El Sidrón specimens analyzed in this study, with their catalogue number, anatomical identification and individuals assignment.
(PDF)

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Author Contributions

Conceived and designed the experiments: AE AR. Performed the experiments: AE. Analyzed the data: AE. Contributed reagents/materials/analysis tools: AE AR. Wrote the paper: AE AR.

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Longstanding dental pathology in Neandertals from El Sidrón (Asturias, Spain) with a probable familial basis

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Pleistocene

ABSTRACT

Two Neandertal specimens from El Sidrón, northern Spain, show evidence of retained left mandibular deciduous canines. These individuals share the same mitochondrial (mtDNA) haplotype, indicating they are maternally related and suggesting a potential heritable basis for these dental anomalies. Radiographs and medical CT scans provide evidence of further, more extensive dental pathology in one of these specimens. An anomalous deciduous canine crown morphology that developed before birth subsequently suffered a fracture of the crown exposing the pulp sometime after eruption into functional occlusion. This led to death of the tooth, periapical granuloma formation and arrested deciduous canine root growth at an estimated age of 2.5 years. At some point the underlying permanent canine tooth became horizontally displaced and came to lie low in the trabecular bone of the mandibular corpus. A dentigerous cyst then developed around the crown. Anterior growth displacement of the mandible continued around the stationary permanent canine, leaving it posteriorly positioned in the mandibular corpus by the end of the growth period beneath the third permanent molar roots, which, in turn, suggests a largely horizontal growth vector. Subsequent longstanding repeated infections of the expanding cyst cavity are evidenced by bouts of bone deposition and resorption of the boundary walls of the cyst cavity. This resulted in the establishment of two permanent bony drainage sinuses, one through the buccal plate of the alveolar bone anteriorly, immediately beneath the infected deciduous canine root, and the other through the buccal plate anterior to the mesial root of the first permanent molar. It is probable that this complicated temporal sequence of dental pathologies had an initial heritable trigger that progressed in an unusually complex way in one of these individuals. During life, this individual may have been largely unaware of this ongoing pathology.

Introduction

Previously, Prieto and Abenza (1999a,b), Prieto (2005), and López-Valverde et al. (2012) have described multiple dental pathologies in an adult Neandertal hemi-mandible (Adult 2; SDR-007/008) from El Sidrón, northern Spain (Fortea et al., 2003). Adult 2 represents one of 13 individuals preserved in the sample from El Sidrón (Rosas et al., 2006, 2012). The mandible is preserved from the left ramus to the mesial aspect of fractured right canine socket, but is missing the posterior border, condyle and coronoid process of the left ascending ramus. López-Valverde et al. (2012) noted several dental abnormalities including a retained left deciduous canine with an anomalous crown morphology, a radiolucent periapical area beneath the mesial root of the left first permanent molar and an unerupted left permanent canine lying low in the mandibular body beneath the second and third molar roots.

Dental pathology in fossil hominins is comparatively rare and this specimen offers an exceptional opportunity to study a number of untreated disease processes that may have accumulated and

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progressed in parallel over the lifetime of the individual. Judged by the completed M3 root apexes and the minimal occlusal wear on the left M3, this individual was a young adult at the time of death but some of these dental pathologies must have arisen before birth and others were acquired or developed gradually over many years.

New medical CT images of the specimen allow us to put together a more comprehensive picture of the dental pathology present in this mandible. It is also now possible to piece together a better chronological history of how these pathologies may have developed over the lifetime of the individual. Moreover, there is now genetic evidence about the familial relationships between some specimens at El Sidrón. Particularly in this respect, an adolescent individual, Adolescent 3, represented only by isolated teeth and a small fragment of mandible, shares the same mtDNA haplotype as the Adult 2 hemi-mandible described here (Lalueza-Fox et al., 2011). This individual also shows evidence of shared dental pathology with the Adult 2 hemi-mandible.

Individual 2 from El Sidrón preserves most of the lower dentition and a complete maxilla has been associated with this individual. It retains, even post-fossilization, severe dental calculus deposits, with the maxillary left premolars and molars either partially or totally covered. There is also an asymmetry in the degree of occlusal wear between the right maxillary dentition, which is more advanced (more evident in the canine), and the left one. Regarding the pattern of para-masticatory dental wear, and despite Adult 2 having a large number of instrumental striations indicating a right-handed preference (Estalrrich and Rosas, 2013), some striations on the anterior teeth are nevertheless distinctive of left-handedness, suggesting some degree of interchangeable hand-use in this individual. This observation may be of relevance in trying to interpret whether or not any occlusal wear asymmetry might derive from one or other of the dental pathologies described in this paper.

Materials/methods

Lateral radiographs, periapical radiographs and medical CT scans (slice thickness 0.625 mm, pixel size 0.344 mm) were made of the Adult 2 Neandertal hemi-mandible, and of the mandibular fragment of the adolescent specimen, and reconstructed in Amira 4 (VSG). Besides these, conventional radiographs were also taken. Additional observations and measurements were made directly on the specimens.

Description of the specimens

The dental pathology of Adult 2; mandible SDR-007-008 Both permanent central incisors are missing from the Adult 2 mandible, lost post-mortem, but both lateral incisors are present (although the left lateral incisor is now removed from the specimen). The permanent left canine is unerupted (Fig. 1) and lies horizontally low in the mandibular corpus. Its incisal tip lies in line with the mesial root apex of the M2 ~15 mm below the alveolar bone margin and ~20 mm above the lower border of the mandible (Fig. 2). The canine root apex lies ~3 mm distal to the distal M3 root apex and protrudes through a fenestration (7 × 10 mm) in the lingual cortical plate of the submandibular fossa, well beneath the mylohyoid line. The canine lies immediately lingual to the inferior alveolar nerve bundle (Fig. 2) but the external contours of the mandibular bone are normal both lingually and buccally. CT scans show that the pulp chamber and pulp canal of the unerupted canine are small and reduced, suggesting an older rather than a younger tooth that has continued to form secondary dentine for some time despite being unerupted and non-functional.

A retained deciduous canine is positioned between the left lateral incisor and the P3 (Fig. 3). The deciduous canine crown is abnormal in its morphology but its root appears normal. The surface enamel immediately above the cervix also appears normal but this part of the crown is somewhat peg-shaped and surmounted occlusally by an additional cap of enamel. The cap expands as a dilatation from a clear constriction where it joins the true crown to form a flat worn surface that was in occlusion with the distopalatal aspect of the upper left canine. Occlusally the crown is ~3 mm wide mesiodistally and has contact facets for the lateral incisor mesially and the P3 distally. It appears to have been tightly integrated into the dental arch and in functional occlusion.

The overall appearance is of a peg-shaped deciduous tooth crown joined head-to-head at a mid-crown constriction with an upper portion set at 90° to the long axis of the main root canal and pulp chamber of the tooth (Fig. 3). On the buccal aspect of the abnormal enamel extension, there is a circular 'crater-like' feature comprising a fractured enamel rim and dentine core with an exposed central pulp horn in its base. A part of the bulbous upper crown extension appears to have fractured off here, leaving an exposed portion of its pulp horn in direct communication with the main pulp chamber and root canal. On CT scans, a continuous rim of enamel surrounds a central dentine core that has fractured through on the buccal aspect at a point where the two pulp horns meet at an isthmus (Fig. 3). The retained deciduous tooth root appears normal and measures ~10 mm long. At the cervix, the root is 3 mm mesiodistally by 4 mm buccolingually in transverse cross-section. However, the root has a wide-open apex and a wide pulp canal consistent with incomplete root formation.

The premolar crowns show no signs of any pre-mortem pathology such as caries, crown fractures or discolouration. Enamel wear facets buccally are only just through to dentine on the P4. The M1 crown shows no signs of any pre-mortem pathology and has only small islands of dentine wear exposed over the buccal cusps. The M2 shows a few enamel wear facets on the cusp tips. On the M3, there are only minimal enamel wear facets. Neither M2 nor M3 shows any evidence of pre-mortem crown pathology, although there are heavy deposits of supragingival calculus on the lingual aspects of M1 and M2 with some evidence of early lingual crestal bone resorption in this position (López-Valverde et al., 2012). On the CT images there are several obvious post-mortem shrinkage fractures through the premolar and molar crowns and roots (Fig. 2).

The bony pathology of Adult 2 Anteriorly, a large buccal sinus (~10 mm by 8 mm) emerges from an extensive bony cavity beneath the roots of the left lateral incisor and deciduous canine (Fig. 1). The alveolar margin of the buccal plate at the top of the sinus opening may have been intact at death since there is fresh fractured trabecular bone mesial to the deciduous canine root. At the buccal opening of the sinus, two bony cavities appear to have coalesced into one. Beneath the incomplete deciduous canine root apex there is a rounded eroded bony cavity typical of a periapical granuloma. Rising up lingually and inferiorly from the floor of the main bony cavity is a separate funnel-shaped sinus that opens low down beneath the lateral incisor root apex to merge with the cavity beneath the deciduous canine root (Fig. 1).

A large mental foramen, typical of Neandertals, opens midway between the mesial and distal M1 roots. This lies 20 mm below the margin of the buccal alveolar bone and 10 mm below the distal M1 root apex. Two small vascular foramina open anterior to the mental foramen, one beneath the mesial M1 root and one higher up beneath the P4 root apex (Fig. 1).

A large buccal sinus with well-established smooth rolled bony margins has exposed the apical two-thirds of the mesiobuccal M1 root (Fig. 1). Some of the crestal alveolar bone from the superior margin of the sinus may have been lost post-mortem, giving the

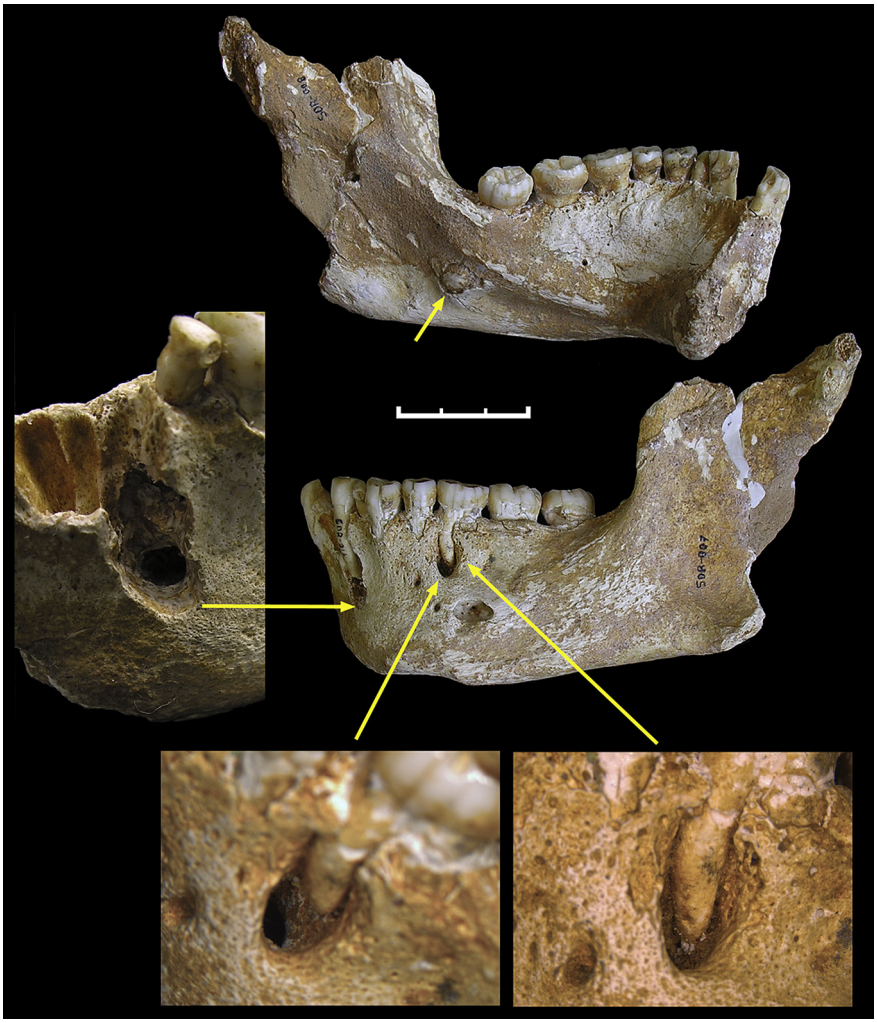

Figure 1. El Sidrón Individual 2 hemi-mandible. Lingually, (top image) the root apex of the impacted permanent left canine is visible protruding through cortical bone beneath the M3 distal root within the submandibular fossa. Heavy calculus deposits are also visible around the premolar and molar cervix. Buccally, (middle right image) the large mental foramen is visible beneath M1 with two accessory foramina mesial to it. Above the mental foramen a large smooth-walled sinus has exposed the mesial root of the M1. The two higher power views below show the sinus tract rising up from beneath the P4 root (bottom right image) but also that some intact bone remains around the apex of the M1 mesial root (bottom left image). Anteriorly (middle image), a second buccal sinus opens deep beneath the socket of the I2 (now removed post-mortem) and this has coalesced with the apical granuloma surrounding the incomplete apex of the deciduous canine.

false impression of a deep infrabony periodontal pocket here. On lateral radiographs it appears that an apical granuloma surrounding the mesial M1 root is the true source of this buccal sinus (Fig. 2). However, much of the M1 root is still surrounded by bone and there is no focal bone loss around the whole of the mesiobuccal root apex. A more likely primary source appears to be a large bony sinus tract that rises from beneath the P4 root distobuccally. Running across the mesial M1 root this has eroded much of the bone overlying it (Fig. 2). Secondary involvement of the M1, however, cannot be ruled out since on some of the CT scan slices (but less clear on lateral radiographs) the distal M1 root apex and its surrounding bone seem to show periapical changes consistent with a non-vital tooth. There is, however, no obvious primary cause for this, such as caries, pre-mortem tooth fracture, tooth discolouration or pulp exposure through wear.

Lingually, beneath the root apices of M3, the apical third of the buried canine root protrudes through an oval 7 mm by 10 mm fenestration in the cortical bone of the submandibular fossa below the mylohyoid line (Fig. 1). Its upper margin is 15 mm below the alveolar crest distal to M3. There is no sign of bone resorption or periapical infection here, i.e., the root apex has maintained a knife-edge rim of bone peripherally. A small pinprick hole 1 mm diameter below the lingual M2 mesial root apex can be seen on CT scans to communicate with a cyst-like cavity within the mandibular body (Fig. 2).

The cyst cavity within the Adult 2 mandible Lateral x-rays show clearly the unerupted permanent canine lying low in the mandibular body. However, López-Valverde et al. (2012) have noted the heavily mineralized bone of this specimen and so as a result there is little evidence on lateral radiographs of any bony pathology within the mandibular corpus. Medical CT scans of the specimen now reveal clearly that the unerupted canine is associated with an extensive cyst cavity within the body of the mandible. This cavity completely surrounds the crown of the canine to its cervix, but not the root, which appears to have a normal but reduced periodontal ligament space. The floor of the cavity is regular in its contour and runs parallel with the lower border of the mandible ~10 mm above it. The roof of the cavity is irregular in outline and runs below the bone beneath the M2 and P3 roots but extends up and between the mesial M1 and P4 roots and is in close association with these roots. The cyst cavity (Figs. 2 and 4) communicates anteriorly with the sinus beneath

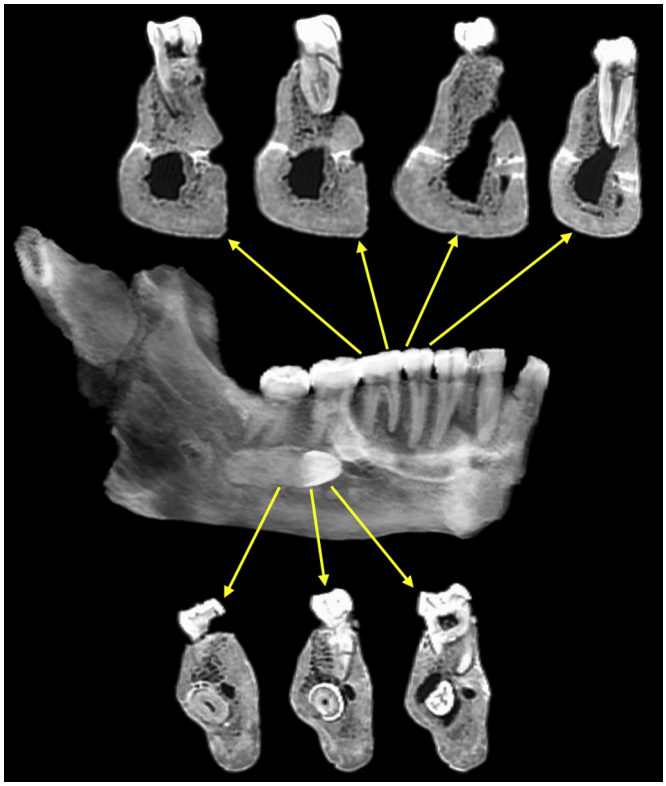

Figure 2. Consecutive CT slices through the left mandibular corpus of El Sidrón Individual 2. The top series are axial slices respectively through the P4, P4/M1 interproximal alveolus, mesial M1 root and distal M1 root. Beneath are consecutive slices through the crown, cervix and root, respectively, of the impacted permanent canine. The inferior alveolar canal lies lateral to the canine and is not involved in the cyst cavity. The crown of the canine lies within the cyst cavity but the cervix and root are surrounded by bone and/or a narrowed periodontal ligament space.

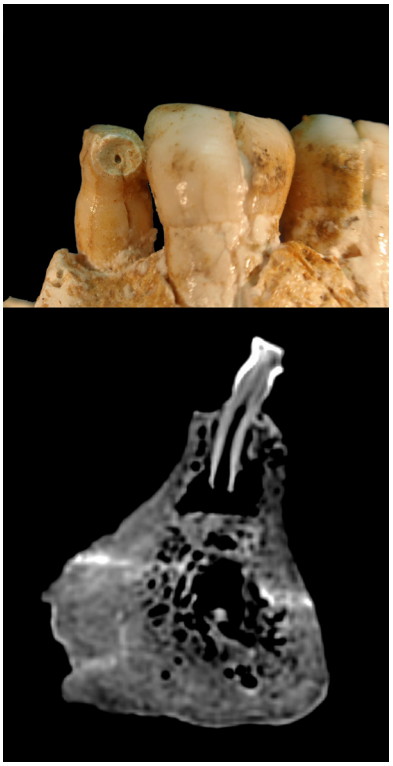

Figure 3. The deciduous canine crown of El Sidrón Individual 2 is abnormal in its morphology. An essentially peg-shaped crown has a flattened worn cap and a buccal extension that has fractured off exposing a pulp horn centrally. This communicates at right angles with the central pulp chamber and root canal of the tooth. The CT image below reveals that the root arrested during development short of its full length with an incomplete and open apex. Surrounding the root apex is a bony cavity resembling that of a typical, but large and longstanding, apical granuloma. Still lower in the image, the anterior projection of the cyst cavity is visible as a central radiolucency within the trabecular bone of the mandibular corpus.

the lateral incisor and deciduous canine roots and also extends buccally beneath P4 to emerge as a second sinus opening through the buccal cortical bone between P4 and M1. There is no obvious erosion or resorption of the roots of any teeth in the mandible. The P4 root in particular appears to be in direct contact with the cyst cavity but has a normal root apex appearance. In places, the bone lining the cavity wall shows evidence of repeated remodelling; regular contours of bone of lower densities follow the cavity boundaries and overlie those of higher densities or vice versa (Fig. 4).

Genetic analyses

Recent genetic analyses support the taphonomic and archaeological hypothesis that El Sidrón represents a synchronic assemblage of a Neandertal family group. Mitochondrial (mtDNA) data suggest that the group was kinship-structured, being the same mtDNA haplotype present in seven out of 12 individuals. The mtDNA diversity inferred from 12 individuals is significantly lower than any random subsample of sequences from unrelated modern Europeans (Lalueza-Fox et al., 2011), taken as a reference for comparison.

Adult 2 and Adolescent 3 are both males and may be related through the female line as they share the same mtDNA haplotype; the one with the highest frequency out of the three detected in the assemblage. A possible kinship between them, in accordance to their relatively similar age, would be brothers or maternal cousins. Other potential maternal relationships (e.g., uncle–nephew, granduncle–nephew) are less likely or can be excluded because of

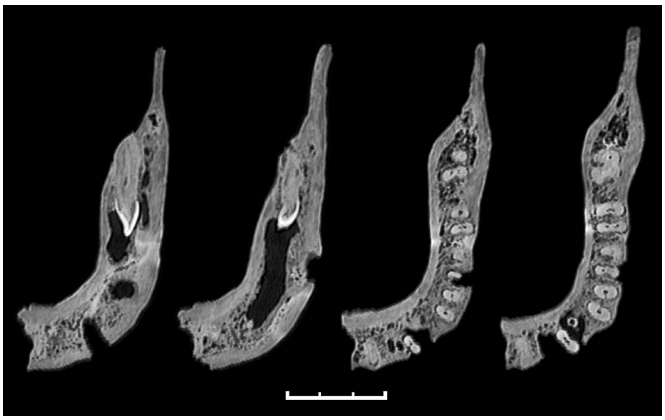

Figure 4. Four consecutive horizontal CT slices through the left corpus of El Sidrón Individual 2 with the lowest on the left and highest on the right. The lowest slice (left) cuts though the permanent canine axially along its length and shows the crown within the cyst cavity but the root surrounded by bone. The inferior dental canal lies just lateral to the canine. The tract of the sinus beneath the P4 is visible centrally and the sinus tract beneath the retained deciduous root anteriorly. The second image from the left shows the full anteroposterior extent of the cyst cavity, the third image from the left shows the opening of the sinus tract beneath the M1 mesial root (still, however, mostly surrounded by bone at its apex) and the image on the right the incomplete deciduous root positioned centrally within the radiolucent space of its apical granuloma now confluent with the cyst cavity.

the age similarity. However, considering the general low mtDNA genetic diversity found in Western European Neandertals (Briggs et al., 2009), it cannot be excluded that some individuals sharing the same mtDNA haplotype in the group might be in fact more distantly related.

Of course the mtDNA relationships are not as informative for family relationships as other types of DNA genotyping. Additional genomic information could clarify in the future the genealogical links between these two El Sidrón individuals. The genetic basis for deciduous canine retention, the consequence of previous amelogenesis defects, possibly has an autosomal origin (Brook, 2009), although some X-chromosome genes associated with dental pathologies are known. Defects in enamel formation create the condition known as Amelogenesis Imperfecta (AI), commonly inherited as an autosomic trait. ENAM mutations appear to be responsible for a big part of the autosomally inherited cases, but genetic studies provide evidence for the existence of at least one further autosomal AI loci (Kärrman et al., 1997). Additionally, it has been suggested that regulatory regions such as microRNAs repressing the ENAM gene could be involved in the inheritance of these anomalous dental traits (López-Valenzuela et al., 2012).

The dentition of Adolescent 3

This individual consists of isolated upper left I1, I2, canine, P3, P4 and two upper molar crowns, M2 and M3 (Fig. 5). The upper M2 has very minimal cusp tip wear facets on the palatial cusps and a minimal elongated polished facet on the mesial marginal ridge, but the M3 has no wear at all. The root was at an early stage of development and the tooth was likely unerupted. There is one additional right M3 crown, similar in morphology with the left one and also without occlusal wear, but with no root preserved.

The upper incisors are both worn through to a dentine edge. The upper left canine has a crown length of 12 mm but with 2 mm or 3 mm of cuspal wear loss that has exposed an island of dentine. This is continuous distally with a very strong wear facet (for the lower P3 mesial occlusal contact facet) along the distal marginal ridge. Mesially there is little more than an elongated polished enamel facet but no wear at all on the mesial marginal ridge. Notably, there is no notched wear facet between the upper left lateral incisor and upper canine for the tip and distal ridge of a lower canine.

The lower teeth preserved are the isolated right P4 and left P4, which is now separate from a small portion of the left mandibular fragment but with only the crown and a small 5 mm portion of its root preserved buccally. The left P3 is still implanted in the mandibular fragment that also contains the socket for the lower left P4 (Fig. 5). The lower left P3 shows slight enamel wear occlusally and more marked wear on its distal slope but has no proximal contact facet for a left lower canine mesially.

A small retained deciduous canine root lies mesial to the P3 but the crown is fractured off transversely post-mortem at the level of the alveolar crest (Fig. 5). This retained deciduous root measures ~5 mm buccolingually by 4 mm mesiodistally at the alveolar crest. On periapical x-rays, the root is 11 mm–12 mm long. No deciduous canine root apex is visible protruding through the fractured base of the alveolar bone fragment beneath.

No lower permanent canine was present in the dental arch. By association, based on an identical pattern of linear hypoplastic banding of upper and lower canines, a lower left permanent canine crown appears likely to belong to the same individual (Fig. 5). This is unworn with a crown height of 14 mm and only 8 mm of fractured root preserved buccally. The pattern of wear in both upper and lower permanent teeth suggests the lower permanent canine was unerupted (or else erupted out of the dental arch and so out of functional occlusion). It seems clear that the deciduous canine was retained with a completed but unresorbed root in this individual.

Discussion

It is recognized that anomalies in size, shape and number of the deciduous dentition are often subsequently associated with anomalies in permanent tooth development (Brook and Winter, 1970; Shah et al., 2007). Brook (2009:S3) has emphasized that the processes underlying many dental anomalies are “multifactorial, multilevel, multidimensional and progressive over time” and that a number of dental defects are known to be heritable. With this in mind, it is logical to discuss the various dental pathologies in these Neandertal specimens in the chronological order that each might have arisen.

Figure 5. Dentition of Adolescent 3 from the El Sidrón site. A. – Occlusal view of the complete preserved dentition. B. – Dental wear of the upper left I2 and canine. C. – Buccal view of the upper and lower canines. Note the identical pattern of linear hypoplastic banding of upper and lower canines. D. – Occlusal fitting of the upper canine and lower first premolar, relating lower and upper isolated dental pieces. E. – Fragment of mandible in which the root of the deciduous canine can be appreciated. On the left side, a permanent canine without any sign of occlusal wear can be seen, denoting a non-erupted condition.

Abnormal deciduous crown morphology

The anomalous crown shape of the retained deciduous canine in the Adult 2 Neandertal would have been determined before birth as the inner enamel epithelium of the tooth germ mapped out the future shape of the enamel dentine junction. This would have been very early in gestation at around 10–15 weeks and before the time initial mineralization of the deciduous canine germ begins. This has been reported to occur in modern humans around 20 weeks gestation (Sunderland et al., 1987).

While fused teeth result from the enamel and dentine of two separate teeth coming together, and geminated teeth from the division of a single tooth germ into a bifid crown (Shah et al., 2007), the anomaly in this Neandertal specimen best resembles a dilated odontome where a part of the crown shows marked enlargement (Thoma and Goldman, 1946). Most often, a dilatation of the inner enamel epithelium beyond the normal outline of the tooth crown invaginates back into the growing tooth germ to form a so-called 'dens in dente' or 'tooth within a tooth' (Beynon, 1982; Alani and Bishop, 2008). In this case, the inner enamel epithelium appears to have expanded into a dilated extension over the cusp tip that has subsequently continued to form enamel over the whole dentine core that contains a pulp chamber with a narrow central isthmus. Clearly, in this individual it did not prevent the normal eruption of the tooth into function. It seems most probable that biting on this tooth resulted in the fracture of a portion of the dilated crown extension buccally exposing the pulp at its isthmus and resulting in pulp necrosis and arrested root development. The stage of deciduous canine root formation suggests this would have been at around 2.5 years of age by modern human standards (Liversidge and Molleson, 2004). Exposure of the pulp to the oral environment and subsequent necrosis and chronic infection usually result in a periapical granuloma formation, and in this case it seems most probably the granuloma became abscessed and then drained via a sinus into the labial gingival sulcus. If the deciduous canine root apex at this age was positioned below the level of lip muscle attachments to the mandible in this region, it is possible a sinus would have tracked through soft tissues and become established as a fistula that communicated externally through the skin of the 'chin'. More commonly, and more likely, is the establishment of a sinus draining low into the labial sulcus intra-orally.

Permanent canine tooth germs first appear as an anlage on the lingual aspect of the deciduous tooth germ (Fig. 6; Broomell, 1897). These tooth germs begin to expand within their follicles that are in turn contained within a bony crypt before birth and before the end of deciduous canine crown completion. They continue to do so well before mineralization of the permanent canine begins at about six months postnatally. It is possible an enlarged anomalous deciduous tooth germ might have displaced the closely associated permanent tooth germ early in its development, which then continued to develop in a more horizontal position than usual. However, teeth fail to erupt for many reasons and this is just one possibility. The fact that two related Neandertals both have retained deciduous canines strongly suggests a genetic component underlying the non-eruption of the left permanent canines in these specimens. This may or may not have been related to the earlier abnormal development of the deciduous crown in one of these individuals, but failure to erupt was certainly a likely trigger for the subsequent cyst that formed around the left permanent canine in Adult 2.

Cysts in the jaws

Unerupted teeth may occasionally develop cysts around their crowns. While this may only happen in one in 100–150 unerupted teeth, the incidence of impacted teeth and dentigerous cysts is near-identical. For example, the incidence of impacted mandibular canines is 3.5% and that of cysts associated with mandibular canines 3.8%. The incidence of impacted mandibular M3s is 48% and that of cysts associated with mandibular M3s 46% (Shear and Speight, 2007).

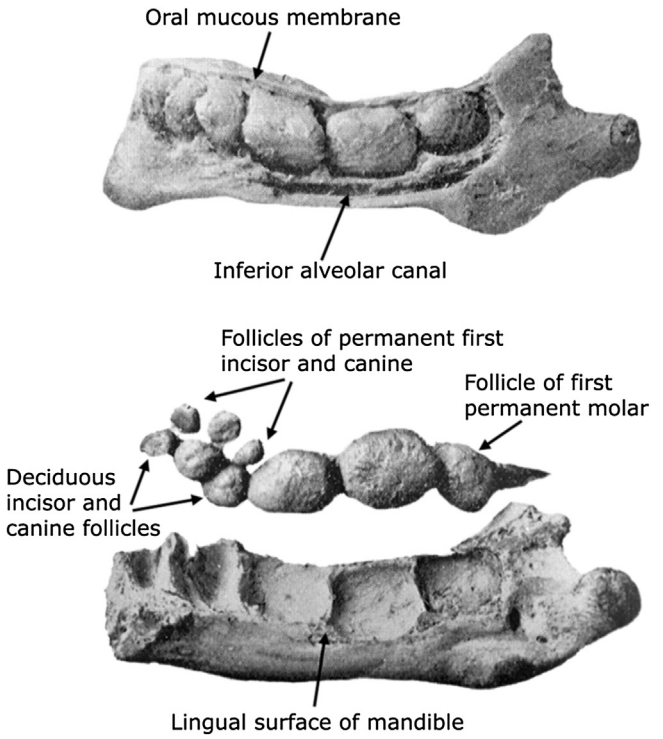

Figure 6. At birth the follicles that contain the developing tooth germs, of all the deciduous teeth as well as those of the permanent anterior teeth and first permanent molar, are present in the jaws. In the upper picture, the lingual aspect of a neonatal hemi-mandible has been dissected to show the follicles of the deciduous teeth and that of M1. In the lower picture, the follicles have been dissected out and rolled over towards the buccal. This reveals the small developing follicles of the permanent central and lateral incisors and the permanent canine. These permanent follicles are positioned lingual to their deciduous counterparts in the jaw but at this age are still attached and closely associated with them. The follicle of the first permanent molar is also present at birth and lies distal to the follicle of the dm2. At this age the dm2 is larger than the M1. (Adapted from Broomell, 1897).

A cyst is a pathological sac-like cavity lined with an epithelium and filled with fluid or semi-fluid like material. Most benign cystic lesions of the jaws tend to increase in size over time because of growth of their lining, increased osmolarity of their contents drawing in more fluid and through bone resorption mediated by many chronic inflammatory products (Toller, 1970; Killey and Kay, 1972; Sandy et al., 1998). Faster growing cysts tend to expand in a spherical manner and have greater bone resorbing activity. Slower growing cysts tend to extend preferentially along the less dense trabecular bone with little resorption or expansion of the dense cortical mandibular or maxillary bone (Killey and Kay, 1972; Sandy et al., 1998).

There are many classifications of benign cystic lesions of the jaws (Shear and Speight, 2007), but the cyst associated with the unerupted permanent canine of Adult 2 most closely resembles a typical dentigerous cyst where the crown of the unerupted tooth is entirely enclosed by expansion of its follicle. Importantly in this classification, the follicle remains attached at the tooth cervix. Nevertheless, another possibility is that this is an example of an odontogenic keratocyst. These cysts are in many ways similar to dentigerous cysts but can only be distinguished for certain by the

nature of their epithelial lining, which is clearly never possible in fossil material. Odontogenic keratocysts, however, are probably genetically determined rather than acquired (Shear and Speight, 2007).

Interestingly with respect to the Adult 2 Neandertal, there is some evidence that many dental cysts may originate from fluid accumulation between one or other layers of the developing tooth germ, either within the stellate reticulum or between the reduced enamel epithelium and the enamel surface. Some enamel hypoplasias may have a similar aetiology. Moreover, anomalous deciduous tooth development and/or inflammation from a deciduous tooth has previously been implicated in initiating some cysts associated with permanent teeth but this has never been substantiated with certainty (Robinson, 1945; Thoma and Goldman, 1960; Bartlett et al., 1973; Atkinson, 1977; Al-Talabani and Smith, 1980; Lustmann and Shear, 1985; Shibata et al., 2004).

Secondary infection of cyst cavities While the primary lesion associated with the unerupted canine in Adult 2 is likely to be a dentigerous cyst, there is clear evidence that this became chronically infected. At death, the picture is of a longstanding and repeatedly infected dentigerous cyst showing evidence of cycles of bone deposition and resorption at its boundary walls. An obvious source of initial infection is the apical granuloma beneath the retained deciduous canine that subsequently became confluent with the cyst cavity anteriorly. Open contact of the cyst cavity with the oral environment would in itself be most likely to lead to repeated bouts of acute inflammation. Other foci of secondary infection are entirely speculative but the sinus from the cyst emerging mesiobuccal to the M1 root was well established and may have tracked along a path of least resistance at the time the deciduous second molar was shed and the P4 was erupting beneath it. López-Valverde et al. (2012) raised the possibility that occlusal trauma led to the death of the M1 pulp that would then have drained directly into the cyst cavity. Were this indeed the case, it might imply that the M1 root fracture (visible in Fig. 2) might have occurred pre-mortem and not post-mortem. However, given the extent of the fracture, it seems likely that at least a portion of the M1 crown would then have been lost during normal masticatory loading during life.

Often, cysts within the jaws only become apparent after many years with no symptoms at all. It is unusual for benign cystic lesions of the jaws to cause pain, paraesthesia or anaesthesia even when they are closely associated with alveolar nerves, unless they become infected. Characteristically, the teeth associated with them are alive (vital) and their pulps do not die even when cysts expand around and between them. But when cysts become infected and drain into the oral cavity, this leads to a continual bad taste and to increased salivary flow rates that are often associated with heavy calculus deposition. As with all infections, especially acute infections, there is then initial tenderness and swelling, quickly progressing to pain and other sensory symptoms from nerve compression. In the case of large cysts, displacement of teeth then makes chewing painful. In this context, the asymmetric pattern of occlusal wear is notable in this individual and perhaps attributable to preferential chewing on the least painful side of the mouth during bouts of acute infection of the cyst cavity. The pattern of alternating left-right handedness noted earlier in this individual may thus sway the explanation of occlusal wear asymmetry away from one due to a strong natural unilateral chewing pattern and towards a more likely one resulting from periods of pain-avoidance. A common eventual mode of clinical presentation of large cysts of the jaws and teeth is unexpected pathological jaw fracture later in life that results from greatly thinned bone from within the jaw.

Mandible growth and displacement of unerupted teeth

The horizontal position of the unerupted canine beneath the M2 and M3 roots would have resulted partly from pressure applied to the crown by the expanding cyst that displaced the tooth distally, but also from growth of the mandible. Growth in length of the mandible occurs primarily at the mandibular condyles, which displaces the mandible anteriorly away from the cranial base (Fig. 7). It is resorption of bone at the chin (and anterior border of the ascending ramus) that then remodels the mandible as it continues to grow in length and width. It seems likely that once the canine was horizontally orientated and became increasingly encapsulated by the growing cyst, it remained low in this developmental position as the bone of the lengthening mandible grew forwards over and around it. Growth in length of the Neandertal mandible was potentially greater than in modern humans today. This in itself may have contributed to the position of the unerupted canine so far distally in the mandible of Adult 2.

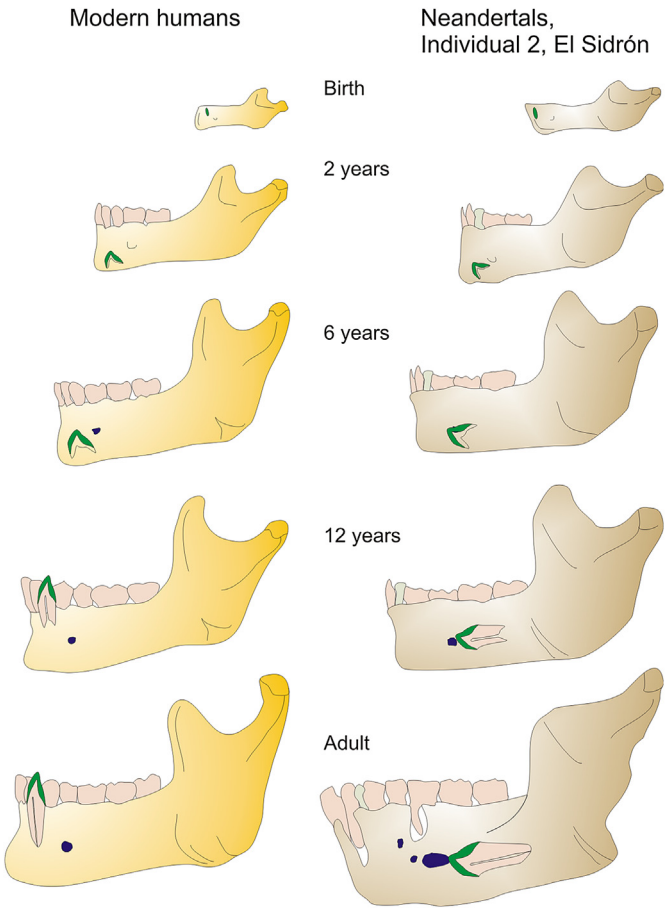

Figure 7. Comparative growth series of mandible and canine development in *Homo sapiens* and the Neandertal, Individual 2 from the El Sidrón. Primary displacement and growth at the mandibular condyle results in lengthening of the mandibular corpus. The follicle containing the permanent canine tooth germ appears before birth just lingual to the developing deciduous canine. With vertical growth of the alveolus, the permanent canine usually comes to lie low in the corpus but remains vertically aligned. As the deciduous canine root is resorbed, the permanent canine then erupts into occlusion. In Individual 2 from El Sidrón, the permanent canine follicle became displaced in the alveolus very early in development tilting the axis of the tooth germ and its follicle anteriorly. Subsequent development of a cyst cavity surrounding the crown of the tooth, together with anterior growth of the mandibular body happening around it, left the permanent canine displaced posteriorly in the adult mandible low in the corpus beneath the M2 and M3 roots.

Coquerelle et al. (2010) have described growth at the mandibular symphysis and of the developing tooth germs contained within the symphyseal alveolar bone in modern chimpanzees and modern humans. While there are clear differences in symphyseal inclination both pre- and postnatally between chimps and humans, the deciduous canines of both maintain a vertical path of eruption and do not appear to be influenced by the anterior, posterior or vertical inclination of the symphysis during mandibular growth (Figs. 5 and 7 in Coquerelle et al., 2010). No such studies exist, however, of the subsequent postnatal development and inclination of the permanent mandibular canine in modern humans and Neandertals. It remains possible that the posterior inclination of the symphyseal region in Neandertals goes hand-in-hand with a more posteriorly inclined permanent canine germ than in modern humans (compare the juvenile from El Sidrón with a modern child in this respect), which might predispose Neandertal permanent canine germs to further horizontal displacement within the jaws more easily than those of modern humans. While this is entirely speculative, it is worthy of consideration since Weinberger (1948) previously illustrated another case of an unerupted left permanent canine and retained deciduous canine in Le Moustier 1 (see also Ponce de León and Zollikofer, 1999). Moreover, Bailey and Hublin (2006) have speculated that the Neandertal remains from Grotte du Renne (Arcy-sur-Cure) include a completely unworn but fully formed canine with substantial cementum deposition at the root apex that may have been impacted or displaced.

Conclusions

Many dental anomalies have a heritable component to them. Here we describe two Neandertal specimens from the same family that both show evidence of retained deciduous canines and unerupted permanent canines. In one, the anomalous deciduous canine crown morphology that developed in utero (at around 10–15 weeks) predisposed it to early crown fracture and exposure of the pulp with periapical infection at ~2.5 years of age. A dentigerous cyst that developed around the unerupted permanent canine, together with anterior growth of the mandible, left it horizontally aligned and distally displaced low in the body of the mandible beneath the M2 and M3 roots. Subsequent bouts of secondary infection from a number of potential sources led to the establishment of two permanent bony sinuses draining the cyst cavity anteriorly beneath the deciduous canine root and buccally between P4 and M1. These examples of dental palaeopathology illustrate how a single genetic predisposition to an anomaly in deciduous tooth formation can progress through a series of subsequently acquired pathological conditions. In this case, they present as a complicated clinical picture post-mortem in a young adult. It is likely that this individual may have been largely unaware of any of this dental pathology during life.

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CAPÍTULO VI - DIVISIÓN DEL TRABAJO EN UN GRUPO NEANDERTAL. SEPARACIÓN DE TAREAS SEGÚN SEXO Y EDAD

Los resultados de este estudio han sido aceptados para su publicación como:

Estalrrich, A., Rosas, A., (aceptado Junio 2014). Division of labor by sex and age in Neandertals: An approach through the study of activity-related dental wear. Journal of Human Evolution.

El estudio del registro arqueo-paleontológico del Pleistoceno Medio y Superior ha proporcionado gran cantidad de evidencias acerca del comportamiento de *Homo neanderthalensis*. Eran principalmente cazadores de presas de tamaño medio y grande (Gaudzinski y Roebroeks, 2000; Hoffecker y Cleghorn, 2000; Patou-Matis, 2000; Richards *et al*., 2000; Bar-Yosef, 2004; Bocheners *et al*., 2005; Speth y Clark, 2006), pero también usaban otros recursos alimenticios como pequeñas presas, comida de origen marino como lapas, diversos vegetales y tubérculos, y se sabe que conocían el fuego y cocinaban su comida (Stringer *et al*., 2008; Henry *et al*., 2011; Blasco y Fernández-Peris, 2012; Hardy *et al*., 2012). Los Neandertales tenían un gran conocimiento del medio natural en el que vivían, usaban plantas medicinales y eran capaces de recorrer

grandes distancias para buscar materias primas para tallar sus herramientas líticas (Santamaría *et al*., 2010; Henry *et al*., 2011; Hardy *et al*., 2012), fueron capaces de cambiar su cultura material (Hublin *et al*., 2012), usaban pigmentos (Soressi y d'Errico, 2007; d'Errico *et al*., 2010; Zilhão *et al*., 2010; Roebroeks *et al*., 2012), enterraban a sus muertos y tenían un comportamiento simbólico (Pettitt, 2002; Rendu *et al*., 2014).

Como cazadores recolectores, los Neandertales deberían tener la misma o similar organización social y estrategias de supervivencia que los cazadores recolectores actuales, lo que implica una división del trabajo según la edad y el sexo de los individuos (Ruff, 1987). Sin embargo, el registro arqueológico no ha aportado evidencias específicas de esta división (por ejemplo, no se han encontrado piedras destinadas a moler y triturar alimentos que son las que tradicionalmente se asocian al trabajo realizado por las mujeres de estos grupos), por lo que se cree que los Neandertales no debieron tener la extrema especialización que aparece hoy en día en estas sociedades cazadoras-recolectoras, al menos en lo que se refiere a la adquisición de comida (Kuhn y Stiner, 2006; Blasco y Fernández-Peris, 2012; Cochard *et al*., 2012). Tanto los hombres como las mujeres Neandertales debían participar en las mismas actividades de caza y de recolección.

En este capítulo se ha planteado el estudio de esta división en otras actividades distintas a la adquisición de comida. En 1973, Murdock y Provost presentaron una serie de actividades que se realizan de manera diferencial entre los hombres y las mujeres de los grupos de cazadores-recolectores, entre otras la preparación de la comida, producción de herramientas o la preparación de

pieles. Estas tareas, entre otras, son responsables de producir marcas distintivas en la dentición del individuo que las realiza (Molnar, 1972; Merbs, 1983; Lukacs y Pastor, 1988; Frayer, 1991; Lalueza-Fox, 1992; Molleson, 1994; Belcastro *et al*., 2004; Scott y Jolie, 2008; Molnar, 2008, 2011; Berbesque *et al*., 2012; d'Incau *et al*., 2012), siendo indicativas de la división del trabajo en poblaciones del pasado.

Por eso se han analizado las marcas encontradas en la dentición anterior del grupo de estudio, y estudiar la variabilidad existente entre individuos de sexo y edad diferente.

VI.1 Metodología

En este estudio se han analizado 99 incisivos y caninos pertenecientes a 19 individuos Neandertales de los yacimientos de la Cueva de El Sidrón (España), Grotte de l'Hortus (Francia) y Grotte de Spy (Bélgica). Estos dos últimos yacimientos han sido descritos en el capítulo 3.

Con el fin de estudiar esta posible división entre los individuos, se han analizado dos tipos de desgaste dental asociado a actividades no masticatorias, y ampliamente descritos en Neandertales: las estrías culturales y las mellas en el esmalte dental.

Las estrías culturales, previamente descritas, han sido ampliamente referidas en Neandertales (Martin, 1923; de Lumley, 1973; Trinkaus, 1983; Bermúdez de Castro *et al*., 1988; Lalueza-Fox y Frayer, 1997; Frayer *et al*., 2010; Volpato *et al*., 2012; Estalrrich y Rosas, 2013).

Las mellas en el esmalte dental son pequeñas fracturas *ante-mortem* que afectan al esmalte o al esmalte y la dentina en su conjunto, en el borde incisal y cara labial de la dentición anterior. Se producen debido a un golpe o presión debido al uso de los diente para el procesado previo de la comida, retoque de herramientas, romper materiales duros, entre otros (Gould, 1968; Molnar, 1971; Merbs, 1983; Belcastro *et al*., 2004; Bonfiglioli *et al*., 2004; Lozano *et al*., 2008; Scott y Winn, 2011).

Las variables que se han considerado en este estudio son el número, longitud y anchura en el punto medio de las estrías culturales; y el número y grado (siguiendo la escala propuesta por Belcastro *et al*., 2004) de las mellas del esmalte dental.

Para ello, los dientes asociados a los individuos de El Sidrón y l'Hortus se han examinado y fotografiado en el MEB de cámara ambiental (ESEM Fei-Quanta 200®) a 100 aumentos. Se han realizado réplicas de alta resolución de los dientes encontrados *in situ* pertenecientes a El Sidrón y de todos los dientes procedentes de la cueva de l'Hortus. El procedimiento en la producción de las réplicas es el mismo empleado en los capítulos anteriores.

Para los individuos del yacimiento de Spy fueron examinados con una lupa binocular de 50 aumentos en el Real Instituto de Ciencias Naturales de Bélgica (Bruselas) y se tomaron fotografías digitales de cada diente.

La longitud y anchura de cada rasgo a estudiar han sido medidas directamente en las fotografías digitales con Image J (Rasband, 2006).

Para estimar la diferencia entre mujeres y hombre en cuanto a la distribución de las mellas del esmalte dental, se ha calculado el número de fracturas por cada diente.

Se ha estudiado la variabilidad de estas variables a lo largo de una única dentición completa y por último, mediante un análisis de la varianza, se han explorado las diferencias entre los individuos.

VI.2 Resultados

En cuanto a las estrías culturales, se ha comprobado que el número de estrías está significativamente correlacionado con el tipo de diente, pero no así la longitud y la anchura de las mismas, de manera que no importa el diente que se estudia a la hora de analizar estas dos variables, pero a la hora de comparar el número de estrías entre individuos, siempre se tiene que compararR el mismo diente, ya que el número de estrías varía según la posición que tenga el diente.

Las estrías más largas aparecen en los individuos El Sidrón Adolescente 2 (femenino), El Sidrón Adolescente 3 (masculino), Hortus IV (adulto joven femenino) y Hortus VIII (adulto joven de sexo desconocido), mientras que las más pequeñas aparecen en El Sidrón Juvenil 1 y El Sidrón Adulto 1 (ambos masculinos) y en Hortus IX (adulto de sexo desconocido).

Las estrías más anchas se han identificado en Spy I y El Sidrón Adulto 1, ambos adultos masculinos, mientras que las más estrechas aparecen en El Sidrón Juvenil 1, y en Hortus X y Hortus XI (ambos adultos de sexo desconocido).

La mayoría de las estrías aparecen en los incisivos centrales maxilares (en 8 de 19 individuos) y el número decrece en los incisivos laterales y los caninos

maxilares. Este patrón también fue descrito por Bermúdez de Castro *et al*., (1988) para los homininos del Pleistoceno medio de la Sima de los Huesos.

Los resultados de la ANOVA muestran que la longitud de las estrías tiene diferencias significativas entre los hombres y las mujeres, siendo las estrías en los dientes de las mujeres más largas. No se han encontrado diferencias entre adultos e inmaduros, ni la anchura tiene ninguna diferencia ni ente hombre y mujeres, ni entre adultos e inmaduros.

Se ha comprobado la variación en el número de estrías en el diente mejor representado en la muestra (ULI1), y se ha encontrado que las mujeres presentan más estrías que los hombres.

Respecto a las mellas de esmalte dental se ha visto que aparecen en menor frecuencia que las estrías. Hay muchos dientes que no tienen mellas, mientras que todos los dientes presentan estrías culturales.

Los hombres tienen sus dientes maxilares con más melladuras (89% de los dientes), mientras que las mujeres tiene más mellas en la dentición mandibular (93% de los dientes). La incidencia de este rasgo es alta en la dentición mandibular de los individuos inmaduros, mientras que en los individuos adultos la incidencia es mayor en la dentición maxilar.

El individuo El Sidrón Adulto 2 no sigue los patrones expuestos ya que tiene el borde incisal completamente mellado.

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Subject: Your Submission

Ms. Ref. No.: T-238R2
Title: Division of Labor by sex and age in Neandertals: An Approach through the Study of Activity-related Dental Wear
Journal of Human Evolution

Dear Almudena,

Many thanks for your prompt revision of your manuscript. You have indeed dealt with the reviewers' minor concerns, thus I am pleased to inform you that your paper "Division of Labor by sex and age in Neandertals: An Approach through the Study of Activity-related Dental Wear" has been accepted for publication in the Journal of Human Evolution.

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Division of labor by sex and age in Neandertals: An approach through the study of activity-related dental wear

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Abstract

The analysis of activity- related dental wear patterns in prehistoric anatomically modern humans and modern hunter-gatherers has shown sex differences attributable to a gendered division of labor. Neandertals are known to have extensive anterior dental wear related to the use of their front teeth as a tool. In this study we analyze the i) cultural striations (scratches on the labial surface of the anterior teeth with a cut-mark morphology), and ii) dental chipping (ante-mortem microfracture involving enamel or both enamel and dentine) in 19 Neandertal individuals from the l'Hortus (France), Spy (Belgium) and El Sidrón (Spain) sites, and compare the characteristics of those traits with the age and sex estimation for the individuals and among samples. The study reveals that all individuals have cultural striations, but those detected on the adult females are longer than the striations found in adult males. Regarding the distribution of dental chipping, the prevalence of this trait is higher in the maxillary dentition of males whereas females have the majority of dental chipping on their mandibular teeth. The differences detected on the overall activity-related dental wear pattern denote a difference or a division of labor by age and sex in Neandertals while using the mouth as a third hand, i.e., in activities other than the provisioning of food, and provides new evidence for the lifestyle of this Pleistocene fossil human species.

Keywords:

l'Hortus; Spy; El Sidrón; Instrumental striations; Dental chipping; Sexual division

Resumen

El patrón de desgaste dental no masticatorio de los cazadores-recolectores prehistóricos y grupos actuales, muestra diferencias según del sexo de los individuos, reflejando una división sexual del trabajo. Los Neandertales, por su parte, tienen un gran desgaste de sus incisivos y caninos debido a que los usarían como coadyuvante o 'tercera mano' en numerosas tareas, como la preparación de pieles o el troceado de pedazos de carne que sujetaban con la boca. En este artículo se presenta el estudio del desgaste dental no masticatorio en 19 individuos neandertales de los yacimientos de l'Hortus (Francia), Spy (Bélgica) y El Sidrón (España). Para ello, se han analizado dos de los rasgos asociados a este tipo de desgaste dental: las estrías culturales (rayas superficiales hechas en la cara labial de la dentición anterior y que tienen la misma morfología que una marca de corte) y las melladuras del esmalte dental (fracturas producidas ante-mortem que afectan al esmalte dental o bien al esmalte y a la dentina en conjunto). Los resultados muestran que todos los individuos presentan ambos rasgos de desgaste no-masticatorio, pero se han encontrado diferencias significativas en cuanto a la longitud de las estrías, siendo más largas en las mujeres. En cuanto a la distribución de las mellas en el esmalte, los hombres tienen una mayor incidencia en la dentición maxilar, mientras que las mujeres es la mandibular. Todas las diferencias detectadas en el patrón de desgaste dental no masticatorio, aunque sutiles, parecen indicar que los Neandertales utilizaban sus dientes de manera diferente según el sexo,

sugiriendo que un cierto grado de división del trabajo ya estaba presente en esta especie humana extinta.

Palabras clave

l'Hortus; Spy; El Sidrón; Estrías culturales; Mellas del esmalte dental; División sexual

Introduction

The analysis of the Middle Paleolithic archaeological record has provided substantial evidence for the Neandertal way of life and behavior. They were active hunters of big game, sometimes even specialized, and top carnivores (Gaudzinski and Roebroeks, 2000; Hoffecker and Cleghorn, 2000; Patou-Matis, 2000; Richards et al., 2000; Bar-Yosef, 2004; Bocheners et al., 2005). They also exploited other resources like marine food, small prey, vegetables, tubers and cooked food (Stringer et al., 2008; Henry et al., 2011; Blasco and Fernández-Peris, 2012; Hardy et al., 2012). Behaviorally, Neandertals utilized an extensive knowledge of their environment (Henry et al., 2011; Hardy et al., 2012), made changes in their material culture (Hublin et al., 2012), and used pigments (Soressi and d'Errico, 2007; d'Errico et al., 2010; Zilhão et al., 2010; Roebroeks et al., 2012) among other examples.

As hunter-gatherers, Neandertals were expected to share the same kind of social organization and survival strategies as modern hunter-gatherers, which implies a partitioning or division of labor between sexes inside the group (Ruff, 1987). However, the lack of grinding stone artifacts and the scarcity of evidence for specific activities linked to modern hunter-gatherer women indicate that Neandertals might not have had such extreme sex-related specialization, at least in terms of the provisioning of food, with both males and females participating in the hunting of big game (Kuhn and Stiner, 2006; Blasco and Fernández-Peris, 2012; Cochard et al., 2012). Still, none of this work answers the question: what was happening after the provisioning of food?

In 1973, Murdock and Provost presented an extensive study describing the gendered separation of specific tasks in different modern hunter-gatherer populations. The tasks included: food preparation, tool production and the preparation of skins. This was the first study to explore specific female/male activities beyond the mere provisioning of food. Several of these activities are known to leave stress marks or enthesopathies on the skeleton (Villotte et al., 2011), while others generate unique non-masticatory dental wear patterns (Lukacs and Pastor, 1988; Molnar, 2008, 2011; Berbesque et al., 2012; d'Incau et al., 2012, among many others).

Activity-related dental wear has been documented , in both historic and prehistoric human populations (Molnar, 1972; Merbs, 1983; Lukacs and Pastor, 1988; Molleson, 1994; Belcastro et al., 2004; Scott and Jolie, 2008; Berbesque et al., 2012). The characteristics and distribution of this type of dental wear within a group or population has the potential to provide information about production activities and the division of labor within those groups or populations (Berbesque et al., 2012). For instance, Bonfiglioli and collaborators (2004) detected, the presence of notching exclusively in males at the archaeological site of Taforalt in Morroco, and Molnar (2008) described females having higher frequencies of horizontal labial striations than males in the

Middle Neolithic population from Ajvide in Sweden. Also, Lorkiewicz (2011) studied the Neolithic populations of the Brześć Kujawski group (Poland) and found statistically significantly differences in the morphology of occlusal grooves, with narrower grooves in females than in males. In addition, in a study of a Medieval population from Greenland Scott and Jolie (2008) found a high incidence of notches on the anterior dentition of females due to the use of their teeth as tools during textile manufacture. All of these gender-based differences in dental wear indicate a sexual division of labor, and the same has been described for the contemporary Hadza hunter-gatherers from Tanzania (Besbesque et al., 2012).

Neandertals are known to have extensively utilized their dentition in non-masticatory activities, such as food preparation, tool production, and preparation of skins (Koby, 1956; Molnar, 1972; Brace, 1975; Puech, 1981; Bermúdez de Castro et al., 1988; Lalueza Fox and Pérez-Pérez, 1994; Lalueza-Fox and Frayer, 1997; Frayer et al., 2010; among others), leaving characteristic wear signatures.

In this study we analyze activity-related dental wear on 99 incisors and canines belonging to 19 Neandertal individuals of both sexes and different ages from three sites [El Sidrón Cave (Spain), l'Hortus (France) and Spy (Belgium)]. The goals here are to shed light on the division of labor by sex and age in this fossil species, and to discuss some possible behavioral implications of these findings. We employ two features commonly found on Neandertal teeth: cultural scratches, and dental chipping. A detailed description of the features and their incidence in Neandertals is provided. In addition to the paleobiological characterization of the sample, we take advantage of the fact that individual sex has been identified for 10 individuals belonging to the El Sidrón cave sample with both morphological and genetic sources of evidence (see Materials and methods).

Activity-related dental wear in Neandertals

Dental wear on labial surfaces has been related to diet as well as to other cultural factors (Molnar, 1971,; Frayer, 1991; Lalueza-Fox, 1992; Lozano et al., 2008; Molnar, 2011; d'Incau et al., 2012, among others). The cultural wear results from individual lifestyles and habits and could be distinguished in most of the cases from dietary microwear mainly on the basis of its larger size (dietary scratches are between 50 to 200 μm in length and width does not exceed 5 μm), and orientation (with a preferred orientation instead of randomness) (Ungar and Grine, 1991; Lalueza-Fox, 1992; Lozano et al., 2008). Because taphonomical erosion of the dental wear features could potentially obscure or delete some or even all of the traits (Teaford, 1988; King et al., 1999), or could make new features that could be misinterpreted as having a cultural etiology (Minozzi et al., 2003; Belcastro et al., 2004), making a clear distinction between ante- and postmortem wear traits is essential in this study.

One of the activity-related dental wear features considered in this study is the so-called cultural, labial or instrumental striations, widely described in Neandertals (Martin, 1923; de Lumley, 1973; Trinkaus, 1983; Bermúdez de Castro et al., 1988; Lalueza-Fox and Frayer, 1997; Frayer et al., 2010; Volpato et al., 2012; Estalrrich and Rosas, 2013, among others). Cultural striations are made when an individual holds

something between his/her anterior teeth with one hand, while with the other hand cuts that item with a stone tool. This behavior is known as 'stuff-and-cut' (Molnar, 1972), and it can accidentally result in scratching of the anterior tooth surface. These marks are defined as a set of striations on the labial surface of the front teeth arranged more or less obliquely to the occlusal plane, and with a cut-mark morphology that differentiates them from dietary striations. The morphological traits of instrumental striations (Fig. 1) are essentially the same as those displayed by cut-marks on bone. That is, presence of linear and parallel edges, a 'V'-shaped section, the presence of Hertzian cones, and parallel microstriations at the bottom of the striation (Shipman and Rose, 1984 for the description of a cut-mark; Bermúdez de Castro et al., 1988; Lozano et al., 2004, for the description of instrumental striations on teeth). The study of the directionality of these striations has allowed some researchers to infer manual laterality in the individuals who have them (Bermúdez de Castro et al., 1988; Lalueza-Fox and Frayer, 1997; Lozano et al., 2008; Frayer et al., 2010; Estalrrich and Rosas, 2013; among others). Depending on the handedness, the striation distribution pattern would be differently oriented.

Cultural striations have also been identified in numerous anatomically modern human populations (Gould, 1968; Molnar, 1972; Merbs, 1983; Molnar et al., 1983; Bermúdez de Castro et al., 1988; Lukacs and Pastor, 1988; Green et al., 1998; Lozano et al., 2008). The fact that the same structure exists in both fossil and extant humans has led to the interpretation that these marks may have the same aforementioned etiology (related to 'stuff-and-cut' behavior; Molnar, 1972), thereby leaving small scratches on their anterior dentition. These tasks are associated with food, fibers or leather preparation, or while cutting meat held between the teeth.

FIGURE 1 SHOULD BE PLACED HERE

Dental chippings are ante-mortem fractures affecting the enamel or both the enamel and dentin, produced during shock or pressure caused as a result of the use of teeth in activities other than mastication of food, or due to hard particles ingested with the food or the use of the teeth to pre-process the food (Belcastro et al., 2004; Scott and Winn, 2011). The marks involving activity-related dental wear may appear only on the incisal edge, mostly on the labial side of each anterior tooth. In contrast, the cracks that appear on the occlusal face of molar and premolar teeth are supposed to be related to a masticatory function (Belcastro et al., 2004; Bonfiglioli et al., 2004) and are not considered on this study.

In order to distinguish between ante-mortem and post-mortem traits, only cracks that appear smoothed, eroded, and with the edges of the fractures rounded have been included in the analyses (Fig. 1), as proposed by Belcastro and collaborators (2004) and Scott and Winn (2011). This type of wear has been previously identified in modern hunter-gatherer populations related to the correction or retouching of stone tool cutting edges (Gould, 1968; Molnar, 1971; Merbs, 1983; Belcastro et al., 2004; Lozano et al., 2008; Scott and Winn, 2011).

Materials and methods

The material under study comprises the incisors and canines associated with 11 Neandertals from the El Sidrón cave (Spain), six individuals from l'Hortus site (France), and the two adults from Spy cave (Belgium). A brief description of the three sites and the paleobiological characteristics of the individuals are provided below and in Table 1.

El Sidrón cave site (Asturias, Northern Spain)

The El Sidrón Neandertal collection is housed at the Department of Paleobiology, at the Museo Nacional de Ciencias Naturales (MNCN- CSIC) in Madrid (Spain). The age of the bone assemblage has been estimated at ~49 kya (thousands of years ago)(Torres et al., 2010; Wood et al., 2013). Currently 13 individuals have been identified: seven adults, three adolescents, two juveniles and one infant (Rosas et al., 2012, 2013). Eleven of them include incisors and canines which were selected for this study (a total of 73 teeth: 69 permanent teeth and four deciduous teeth).

Age at death was estimated based on the inter-individual differences in dental development (AlQahtani et al., 2010) for the immature individuals and, differences in dental wear for adult individuals (following the scale of occlusal dental wear stages proposed by Skinner,, 1997).

Sex was estimated by means of three different methodologies. The first one consists of the analysis of mandible size, following the criteria proposed by Rosas and collaborators (2002) for the Atapuerca-SH hominids mandibles. The second methodology consists of the classical anthropological technique of classifying individuals based on their canine tooth size, and the last methodology is a Y-chromosome assay. A detailed description of the methodology and results of sex-estimation is provided by Lalueza-Fox et al. (2011).

The resulting sample from El Sidrón studied here is comprised of three adult males, three adult females, one adult with sex not yet determined, two adolescent males, one adolescent female, and one juvenile male (see Table 1). All specimens have instrumental striations on their anterior dentition (Estalrrich and Rosas, 2013).

l'Hortus cave site (France)

The site comprises bone remains from a minimum number (MNI) of 20 Neandertal individuals (de Lumley, 1973) dated to the Würm glaciation. The fossils are housed at the European Center for Prehistoric Research in Tautavel (France). From the individuals described by de Lumley (1973), only six (a total of 16 teeth) have been selected for this study: Hortus IV, Hortus VII, Hortus VIII, Hortus IX, Hortus X, and Hortus XI. Regarding their age at death, Hortus IV, Hortus VII, Hortus VIII and Hortus IX are young adults (15 to 30 years old) and Hortus X and Hortus XI are middle-aged adults (30 to 50 years old). From this sample, only individual Hortus IV has been identified as a possible female, whereas sex identification for the others remains unclear (de Lumley, 1973).

Spy (Jemeppe-sur-Sambre, Belgium)

The Spy fossils are housed at the Royal Institute of Natural Sciences in Brussels, Belgium. The fossil assemblage has been dated to approximately 36 kya (Semal et al., 2009, 2011) directly on Neandertal bones and teeth. Adult individuals Spy 1 and Spy 2 were selected for this study (10 teeth). According to Schwartz and Tattersall (2002), both Spy adults could be identified as males due to their anatomical morphology, but according to the endocranial volume, Spy II could be a female (Holloway et al., 2005). Recently Chapman et al. (2013) reconstructed the skeleton of Spy II, stating that this individual was in fact a male. At the moment, a complete revision of individual sex characterization is being developed (P. Semal, Personal communication).

TABLE 1 SHOULD BE PLACED HERE

Microscopic visualization

Teeth belonging to the individuals from El Sidrón and l'Hortus were examined and photographed using a Fei-Quanta Environmental Scanning Electron Microscope (ESEM) located at the National Museum of Natural Sciences (MNCN-CSIC) in Madrid.

The majority of the El Sidrón teeth were found isolated, so they could be observed directly on the microscope. But some of them are on their respective mandible and maxilla, and due to ESEM chamber dimensions, it was necessary to make high-resolution replicas. The same as with l'Hortus teeth, the replicas were made following established procedures (Bromage, 1987; Teaford and Oyen, 1989; Martínez-Maza et al., 2011; Estalrrich and Rosas, 2013). Hydrophilic vinyl polysiloxane was employed to make the negative cast, and polyurethane resin to make the replica. Finally, the replicas were covered with a thin layer of metallic gold (Sputter Coater, EMITECH K550Y®) to allow the ESEM visualization.

All images were taken with tooth wear surfaces perpendicular to the electron beam in order to avoid size and form deformation (Gordon, 1988), at a 100x magnification to allow the appropriate visualization of the wear features and measurement of the traits.

For the Spy Neandertals, the labial surface of each tooth was examined with a binocular microscope at the Royal Belgian Institute of Natural Sciences (Brussels) and then captured as a digital picture at 50x magnification.

In order to be rigorous, we have considered only the striations that have an undoubted cut-mark morphology, that is we excluded from the study the scratches that appear worn (cut-mark morphology is almost removed, and thus we cannot be sure about their origin), and those that are short and thin that could be confused with dietary dental microwear (Ryan and Johanson, 1989; Ungar and Grine, 1991; Pérez-Pérez et al., 1999, among others).

Data acquisition and intra-observer error

Concerning instrumental striations, three variables were considered in this study: the number of instrumental striation on each tooth, and the mean length and mean width of scratches on each tooth. In all cases, width and length of the instrumental striations were measured on digitized images using NIH freeware Image J (Image Processing and Analysis in Java, version 1.41, Rasband, 1997–2008). Width was measured at the mid-point of the instrumental striations.

All measurements were conducted by a single observer, and repeated after several weeks to minimize intra-observer error. Intra-observer error was calculated by the mean absolute percentage difference (MASP) proposed by Grine and collaborators (2002) for microwear studies. This value is calculated as the difference between the observed value and the sample mean divided by the value of the sample mean, all given as a percentage. The MASP we obtained for the different variables studied was: 7.0% for the number of striations, 3.6% for the striation length, and 0.8% for the striation width.

Dental chipping was recorded following the three stages proposed by Belcastro et al. (2004), in which stage 1 corresponds to a small fracture (less than 0.5 mm involving a thin layer of enamel), stage 2 implies an increase in the quantity of enamel affected (around 1 mm), and stage 3 is characterized by a large fracture involving both enamel and dentine (more than 1 mm) that eventually could destroy the tooth. We also recorded the location of the affected areas (mesial, distal, buccal). In order to search for differences between females and males in the distribution of dental chipping, the frequencies (number of factures per tooth) and incidence were estimated.

Statistical analyses

In order to determine if the data from the three sites could be treated as a unique sample, and prior to any other analysis, a comparison of group means of length and width of the scratches from the three sites (Spy, l'Hortus and El Sidrón) was made. Non-parametric Kruskal-Wallis H tests were performed on length and width, with site as the variable (Length: Kruskal-Wallis test: H (2, N= 19) =2.687081 p =0.2609 Chi-Square = 2.773232, df = 2, p = 0.2499; Width: Kruskal-Wallis test: H (2, N= 19) =2.135407 p =0.3438 site Chi-Square = 2.773232, df = 2, p = 0.2499). The results indicate that all data could be considered as a unique sample. Next, different sets of statistical analyses to assess variability within the sample.

The first statistical test, considering the whole sample from the three sites, was designed to detect differences among the variables (number of striations, length and width) depending on the tooth type within the same individual. For this purpose, non-parametric correlation tests (Spearman's rho and Kendall's tau; p-value < 0.05) were used to compare number, length and width of the instrumental striations against tooth type (rank= tooth class) in an individual with the associated anterior dentition almost complete. We have considered 12 categorical ranks: upper right canine (rank 1), upper right lateral incisor (rank 2), upper right central incisor (rank 3), upper left central incisor (rank 4), upper left lateral incisor (rank 5), upper left canine (rank 6), lower right canine (rank 7), lower right lateral incisor (rank 8), lower right central incisor

(rank 9), lower left central incisor (rank 10), lower left lateral incisor (rank 11) and lower left canine (rank 12).

In light of the obtained results (see below), another set of statistical analyses focused on assessing differences in two variables (length and width are not tooth type dependant, according to our results) among Neandertal populations when the individuals were grouped based on their paleobiological categories (Age: adult and immature; Gender: male, female. Individuals with unknown gender were excluded for last analysis). For this purpose, data were ranked transformed to avoid violating assumptions associated with parametric statistical tests. Data for the two variables were compared among the different groups using an analysis of variance model (ANOVA).

Because the number of instrumental striations varied depending on tooth type (see Results section), comparisons were made using the same tooth for all individuals. Non-parametric correlation tests were used to compare the number of striations per tooth type, depending on age and gender. Also, in order to study the variation between the left and right side of the anterior dentition within the same individual, a Wilcoxon Matched Pairs Test was used for this analysis. The sub-sample selected for this analysis comprises 18 paired teeth, all them are permanent teeth.

All results were considered significant when $p < 0.05$.

Results

A summary of the descriptive statistics for the instrumental striations on the Neandertal sample is shown in Table 2. The longest striations (more than 2 mm) have been found in the El Sidrón Adolescent 2 (female) and Adolescent 3 (male), and Hortus IV (young adult female) and VIII (young adult with unknown gender), whereas the smallest (less than 550 μm) appeared on El Sidrón Juvenile 1 and Adult 1 (both males) and Hortus IX (sex unknown). Examples of these specimens are shown in Figure 2.

TABLE 2 SHOULD BE PLACED HERE

FIGURE 2 SHOULD BE PLACED HERE

The widest (more than 70 μm, Figure 3) striations were identified on Spy I and El Sidrón Adult 1, both adult males, while the narrowest (less than 20 μm, Figure 3) appeared on El Sidrón Juvenile 1, Hortus X and XI, both adults with unknown sex.

FIGURE 3 SHOULD BE PLACED HERE

A consistent distribution pattern arises from our results. The majority of the striations appear on both upper central incisors (in eight of the 19 individuals) , as Bermúdez de Castro et al., (1988) described for their Middle Pleistocene hominins sample, while the number of striations decreases in the upper lateral incisors and canines. A more equal distribution appears on the mandibular anterior teeth. The maximum number of striations per tooth on the sample (N = 39 on an upper right

lateral incisor) has been found on Hortus VII and El Sidrón Adolescent 2. Correlation tests show that the number of instrumental striations varies depending on the tooth type (Table 3) within the same individual (there are fewer instrumental striations on the lower dentition), but length and width did not show a statistically significant variation. Thus, for the next analyses we decided to use just those last measures.

TABLE 3 SHOULD BE PLACED HERE

The results of the ANOVA tests show that length is statistically significantly different between females and males, with longer striations in the female dentition (Table 4). In contrast, no statistically significant differences are found regarding the width of the instrumental striations among females and males, or the width and length between immature or adult individuals.

TABLE 4 SHOULD BE PLACED HERE

In order to assess the variation in the number of striations per tooth, a correlation test was used, and tested on one upper left central incisor, which is the most represented tooth within the sample. The results show that the number of instrumental striations is higher in females than in males, and that the number of striations is not correlated with age (Table 5). In this part, only individuals preserving this tooth were analyzed. Also, we checked the right-left intra-individual asymmetry on striation number, and the results show no statistically significantly difference in the individuals analyzed (N=18; T=70.5; Z= 0.653; p-value= 0.514).

TABLE 5 SHOULD BE PLACED HERE

FIGURE 4 SHOULD BE PLACED HERE

Regarding dental chipping (Figure 4), its incidence is lower when compared with cultural striations, as is detailed in Table 6. For the analysis of this trait by means of an individual's sex identification, El Sidrón Adult 7 and Adolescent 2, as well as all individuals from l'Hortus except Hortus IV, were excluded. Our results show that males have more dental chipping on their maxillary dentition (89% of teeth are affected) whereas females have the majority of dental chipping on the mandibular teeth (93% of teeth are affected) (Table 7). The incidence of this trait on immature individuals is also higher in mandibular teeth, whereas in mature individuals the frequency is higher in maxillary teeth. Figure 5 shows the distribution of chipping depending on tooth type when the age and sex of the individuals are considered. The pattern that seems to emerge is that female mandibular teeth are more affected, while male upper incisors and canines are more affected. Immature individuals have their left mandibular teeth and upper incisors affected, in contrast to mature individuals, who have their right mandibular teeth more affected than the left teeth, whereas the upper dentition has the same distribution as immature individuals but with less incidence.

TABLE 6 SHOULD BE PLACED HERE

TABLE 7 SHOULD BE PLACED HERE

FIGURE 5 SHOULD BE PLACED HERE

While the norm in the sample is to have few chips, individuals Sidrón Adult 2 and Hortus VII display a continuous presence of this trait along the incisal plane (see Figure 4).

Discussion and conclusions

As mentioned in the Introduction, some studies on activity-related dental wear have found evidence of a division of labor in past modern human populations (Bonfiglioli et al., 2004; Molnar, 2008; Lorkiewicz, 2011).

In the Neandertal samples analyzed here, the fundamental observation is that all of the individuals present instrumental striations and dental chipping, regardless of provenance, age and sex. Thus, similar behaviors could be expected among them, with all members of the groups performing tasks involving their teeth as tools, and leaving similar type of marks.

Our results show that the number of instrumental striations varies depending on tooth position. Surprisingly, we found no statistically significant difference between right and left teeth from the same individuals, although we were expecting some degree of difference that could be an indicator of the skills the individual possess or even his/her preference while cutting or handedness. The lack of an asymmetrical pattern (no statistically significant differences between right and left dentition) could indicate that the number of striations might be affected by the nature of the item (great variability of items) they were cutting, personal choices, abilities, or a combination of all. However, when considering the whole dentition, we found that maxillary teeth have the majority of the striations, and mandibular teeth have less in comparison. Interestingly, the Neandertals studied here have higher numbers of instrumental striations per tooth than Middle Pleistocene *Homo* and modern human groups (Lozano et al., 2008). It is possible that midfacial prognathism, bigger maxillary teeth, and edge-to-edge occlusion, so characteristic of Neandertals (Trinkaus, 2003; Rosas et al., 2008; Clement et al., 2012, among others), acted as determinants of spatial tooth position, over-exposing the maxillary teeth to damage as our results suggest.

The highest number of striations appear on the maxillary right central incisor from Hortus VII and El Sidrón Adolescent 2. Both are young individuals (see Table 1) and because this dental wear feature is cumulative, it was expected that more striations would be found on older individuals. However, no significant correlation was found between the number of striations and age. It is possible that some of the striations have been erased due to the lips and saliva action, food ingestion, as has been demonstrated for dental microwear (Grine, 1986; Romero et al., 2012). Interestingly, the number of striations appears to be correlated with sex, where females have more striations than males.

The ANOVA test results reveal that there is a statistically significantly difference in the length of the instrumental striations when individuals were grouped by sex. Adult

females have longer striations than adult males. However, no other significant difference was detected.

In light of the results discussed above, it seems that all Neandertals in our sample used their anterior dentition for non-masticatory activities, regardless of their age and sex. However, subtle differences have been found among them. The females have more striations than males, and the striations are longer. Since the instrumental striations are related to a 'stuff-and-cut' behavior (Molnar, 1972), and extrapolating those data to a possible behavioral situation, all individuals likely employed similar lithic instruments (width shows no variation), but task processing, the nature of the material they were cutting (for example stringy versus soft meat they could have cut to ingest), and the repetition were different depending on the gender. That could mean a separation between sexes, or a sexual division of labor in activities other than foraging. In modern hunter-gatherers this kind of separation is present, as Berbesque and collaborators (2012) noted in the dentition from the Hadza (Tanzania) hunter-gatherers. Although their study shows differences in occlusal wear, it is demonstrated that the use of the mouth as a third hand could show sexual differences and therefore, patterns of sexual division of labor, as seems to occur in the Neandertals in our study. Some of the activities that may be underlying these differences could be the preparation of skins, spinning and manufacture of leather products or clothing, which are more frequently performed by females in modern hunter-gatherer societies (according to Murdock and Provost, 1973).

Despite no significant differences being detected in striation width in these samples, the narrowest striations appear on a juvenile individual from the El Sidrón sample, and that could imply that young individuals used tools with a smaller edge than older individuals. The other individual with narrower striations is Hortus IX, a young adult (according to de Lumley, 1973). Other possibilities that can explain the difference in the width among the individuals could be that they had used lithic tools with different cutting edges, or that the stroke during the cutting process could have varied, maybe due to the task they were about to perform, and thus making highly variable striations. Maybe this variation is just reflecting the preference of the individuals for a particular tool.

We cannot exclude the occurrence of both possibilities, so it is necessary to explore this situation in other Pleistocene hominids, in addition to modern hunter-gatherers, in which the individual age and sex could be reliably known.

Another important point regarding the possible division of labor by age is that El Sidrón Juvenile 1 exhibits the same features of activity-related dental wear as adults and adolescents, indicating that this individual had a similar behavior as the other members of the group. Perhaps, taking into account the number, length and width of the instrumental striations described on his anterior dentition, as well as its slightly curved morphology (Estalrrich and Rosas, 2013), it could be possible that the role of this individual within the El Sidrón Neandertal group could be as an apprentice learning how to use his mouth as a third hand, as is the situation in juveniles from hunter-gatherer societies (Bogin, 1999; Marlowe, 2005; Hewlett et al., 2011).

In addition to what emerges from the study of instrumental striations, dental chipping also shows a consistent sexual pattern in the analyzed sample. In this group, females display a higher incidence of this trait on their mandibular teeth, while males show a higher prevalence on their maxillary teeth (see Table 6). As the dentition of the individuals is not complete, the differences detected in the frequencies of dental chipping could not be completely assessed. Several studies (Bonfiglioli et al., 2004; Scott and Winn, 2011) indicate that populations with an intense use of their anterior dentition as a third hand are more likely to have a high incidence of chipping on their maxillary dentition when compared to the mandibular dentition, in both females and males, mature and immature individuals. Yet the fact that this pattern is found on both Spy and El Sidrón Neandertals allows us to propose that this distribution could be somehow common in Neandertals. In these Neandertals, males seem to follow the pattern provided based on ethnographic studies (Bonfiglioli et al., 2004; Scott and Winn, 2011), but females do not. This could mean that these Neandertals performed a different behavior than what has been described for historic and pre-historic populations.

Regarding the distribution of chipping by age, the percentage of chipped teeth on immature Neandertals is higher when compared with mature individuals. As the former have fewer teeth assigned and are fewer in number, the results presented here must be considered with caution. The differences could be due to both differences in sample size or a separation or division of tasks between young and old Neandertals. Nevertheless, more chipped teeth does not imply more chips on average, since two adult individuals, Hortus VII and El Sidrón Adult 2, both have the highest incidence of chips on their teeth. While El Sidrón Adult 2 has his whole anterior maxillary dentition full of microfractures (exhibiting a 'nibbling' effect, Estalrrich et al., 2013), Hortus VII has just one tooth extremely affected (see Fig. 5). Only two individuals from the whole sample, each one from a different site, have the same elevated incidence and could mean an exceptionally specialized behavior within the groups. In the case of El Sidrón Adult 2, we have additional evidence about his paleobiology. Dental pathologies on the left side of the mandible, as well as severe calculus deposits located occlusally on both maxillary and mandibular second and third molars (Dean et al., 2013), and the change in cultural striation orientation (Estalrrich and Rosas, 2013), may suggest that holding items between his teeth and cutting them could be perhaps painful. Bitumen or oil shale has been recovered from his dental calculus, the only one from his group (Hardy et al., 2012). Bitumen has been described as a hafting material during the Middle Paleolithic (Boëda et al., 1996). All of the peculiarities surrounding El Sidrón Adult 2 reinforce the idea that this individual may have had a specialized behavior within his group, in which, for example, he could have used his front teeth to haft stone points onto wooden spears or handles (for what he would have used bitumen), leaving the dental chipping and the bitumen traces. We could not be sure about Hortus VII since the dentition is not complete, and no other traces of his/her behavior are yet known.

Several studies are improving our knowledge about the complexity of Neandertal behavior [organizational patterns of activity areas (Vallverdú et al., 2010, 2012), land use (Daujeard and Moncel, 2010), symbolic artefacts in the Neandertal material culture (Bailey and Hublin, 2006; Caron et al., 2011), genetic fluxes and

behavioral mating (Lalueza-Fox et al., 2011), and the use of medicinal plants and bitumen (or oil shale) though the study of dental calculus (Hardy et al., 2012)]. Here we add on the potential division of labor giving a new twist on the apparent 'modern' behavior of these archaic humans.

The results presented here illustrate how Neandertals used their mouth as a third hand, and may indicate some subtle differences suggesting individual roles within the groups.

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Figure Captions

Figure 1. Activity-related dental wear features on Neandertal teeth. Left: a cultural striation on a lateral lower incisor from El Sidrón cave with the characteristic cut-mark morphology. Middle: post-mortem fracture (not considered on this study) on a mandibular central incisor. Right: ante-mortem crack or dental chipping on a maxillary canine.

Figure 2. Length variation of cultural striations within the Neandertal sample. On the top are the longest: El Sidrón Adolescent 2 (left), El Sidrón Adolescent 3 (middle), Hortus VIII (right). At the bottom are the smallest of the sample: El Sidrón Juvenile 1 (left), El Sidrón Adult 1 (middle), Hortus IX (right). All images were taken with an ESEM.

Figure 3. Width variation of cultural striations within the Neandertal sample. On the top are the widest instrumental striations. Spy I (left, a binocular microscope image), and El Sidrón Adult 1 (right, an ESEM image). At the bottom are the narrowest instrumental striations found in the sample: El Sidrón Juvenile 1 (left), Hortus X (middle), and Hortus XI (right), all are ESEM images.

Figure 4. Examples of dental chipping on the Neandertal teeth: Hortus VII (on the top, left side), with a grade 2 lesion; Spy X (on the top, right side), with a grade 1 lesion; El Sidrón Adult 5 (in the middle, left side) with a grade 2 dental chipping; El Sidrón Juvenile 1 (middle, right side) also with a grade 2 lesion; and below, El Sidrón Adult 2 upper left central incisor as an example with numerous chips on the incisal edge (on the right side, a close-up of the central part of the incisal margin).

Figure 5. Histograms showing the dental chipping frequencies for: A) females and males depending on tooth type (the sample comprises only the individuals with known sex characterization from all sites); and B) dental chipping frequencies by tooth type and the estimated age at death. The categories considered are mature (=adults) and immature (=adolescent and juvenile), and all individuals from the sample are included.

Table 1. Summary of the paleobiological features of the Neandertal individuals analyzed from L'Hortus (de Lumley, 1973), Spy (Holloway et al., 2005; Chapman et al., 2013) and El Sidrón (Lalueza-Fox et al., 2011; Rosas et al., 2012, 2013). In addition to the standard anthropological techniques used to sex the individuals, paleogenetic analyses for El Sidrón Neandertals (Lalueza-Fox et al., 2011), and brain endocast volumes for Spy Neandertals (Holloway et al., 2005) were also applied.

INDIVIDUAL	SITE	SEX	AGE	MAXILLARY TEETH	MANDIBULAR TEETH	TOTAL TEETH
EL SIDRÓN-ADULT 1	El Sidrón cave	male	young adult	LC; LI2; LI1; RI1; RI2; RC	LC; LI2; RI1; RI2; RC	11
EL SIDRÓN-ADULT 2	El Sidrón cave	male	young adult	LC; LI2; LI1; RI1; RI2; RC	LI2; RI1; RI2	9
EL SIDRÓN-ADULT 3	El Sidrón cave	female	middle-aged adult	LC; LI2; RI2; RC	RI1; RI2	6
EL SIDRÓN-ADULT 4	El Sidrón cave	female	adult	LC; LI1	LC; LI2; LI1; RI1; RI2; RC	6
EL SIDRÓN-ADULT 5	El Sidrón cave	female	middle-aged adult	LC; LI2; LI1; RI1; RI2; RC	LC; LI2; LI1; RI1; RI2	11
EL SIDRÓN-ADULT 6	El Sidrón cave	male	middle-aged adult	LC; LI1	LC; LI2	4
EL SIDRÓN-ADULT 7	El Sidrón cave	unknown	middle-aged adult	RI2; RI1	RI2	3
EL SIDRÓN-ADOLESCENT 1	El Sidrón cave	male	11-15 years old	LC; RC	RI1; RI2	4
EL SIDRÓN-ADOLESCENT 2	El Sidrón cave	unknown	12-15 years old	LI1; RI1; RI2	RI2; RC	5
EL SIDRÓN-ADOLESCENT 3	El Sidrón cave	male	12-15 years old	LC; LI2; LI1	LC	4
EL SIDRÓN-JUVENILE 1	El Sidrón cave	male	Approx. 7.5 years	LI1; dRc; RI1	LI1; dLc; RI1; dRi_2; dRc	8
HORTUS IV	Grotte de l'Hortus	female	young adult		LC; RC	2
HORTUS VII	Grotte de l'Hortus	unknown	young adult	LI1; RI1; RI2		3

HORTUS VIII	Grotte de l'Hortus	unknown	young adult	LC; LI2; LI1; RI1; RI2; RC		6
HORTUS IX	Grotte de l'Hortus	unknown	young adult	LC; LI1		2
HORTUS X	Grotte de l'Hortus	unknown	adult	LI2; RI1		2
HORTUS XI	Grotte de l'Hortus	unknown	adult	RI2		1
SPY 1	Grotte de Spy	male	adult	LI2; RI1; RC	LI2	4
SPY 2	Grotte de Spy	male	adult	LC; LI1; RC	LC; LI1; RI2	6

Figure 1

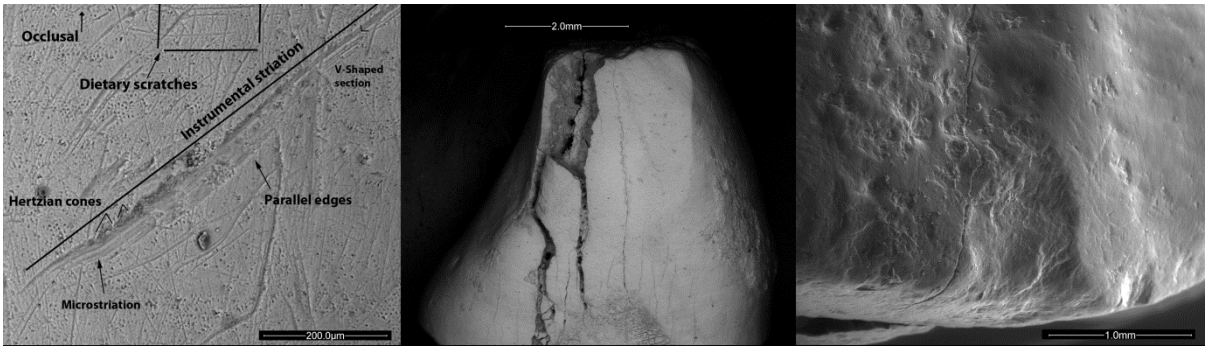
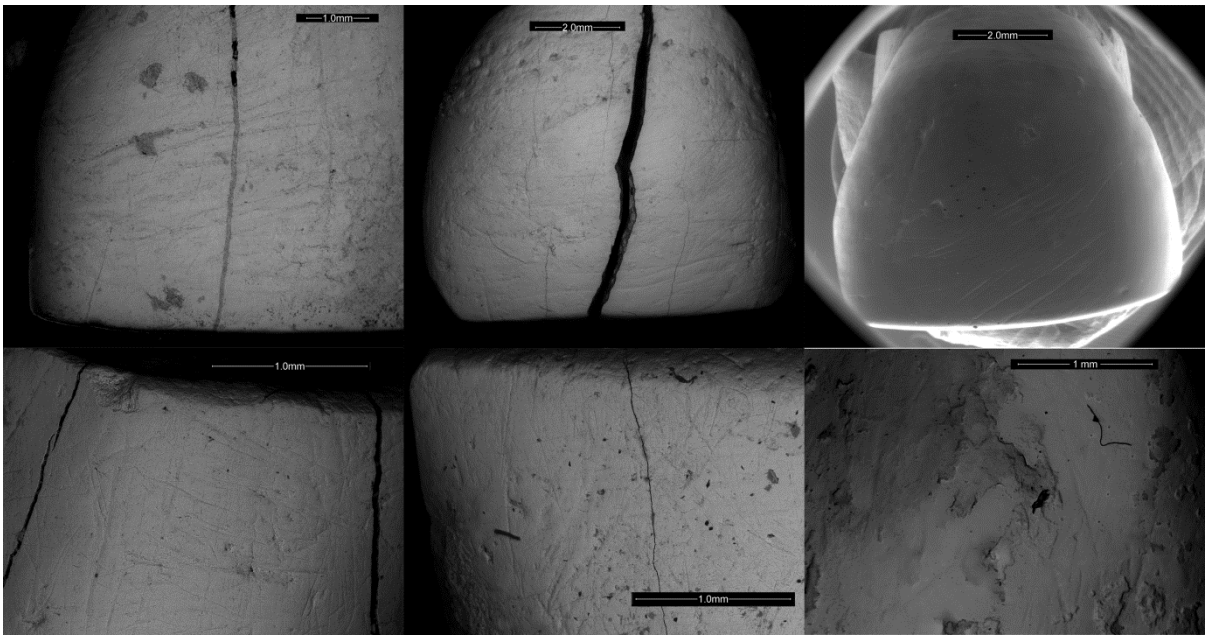


Figure 2



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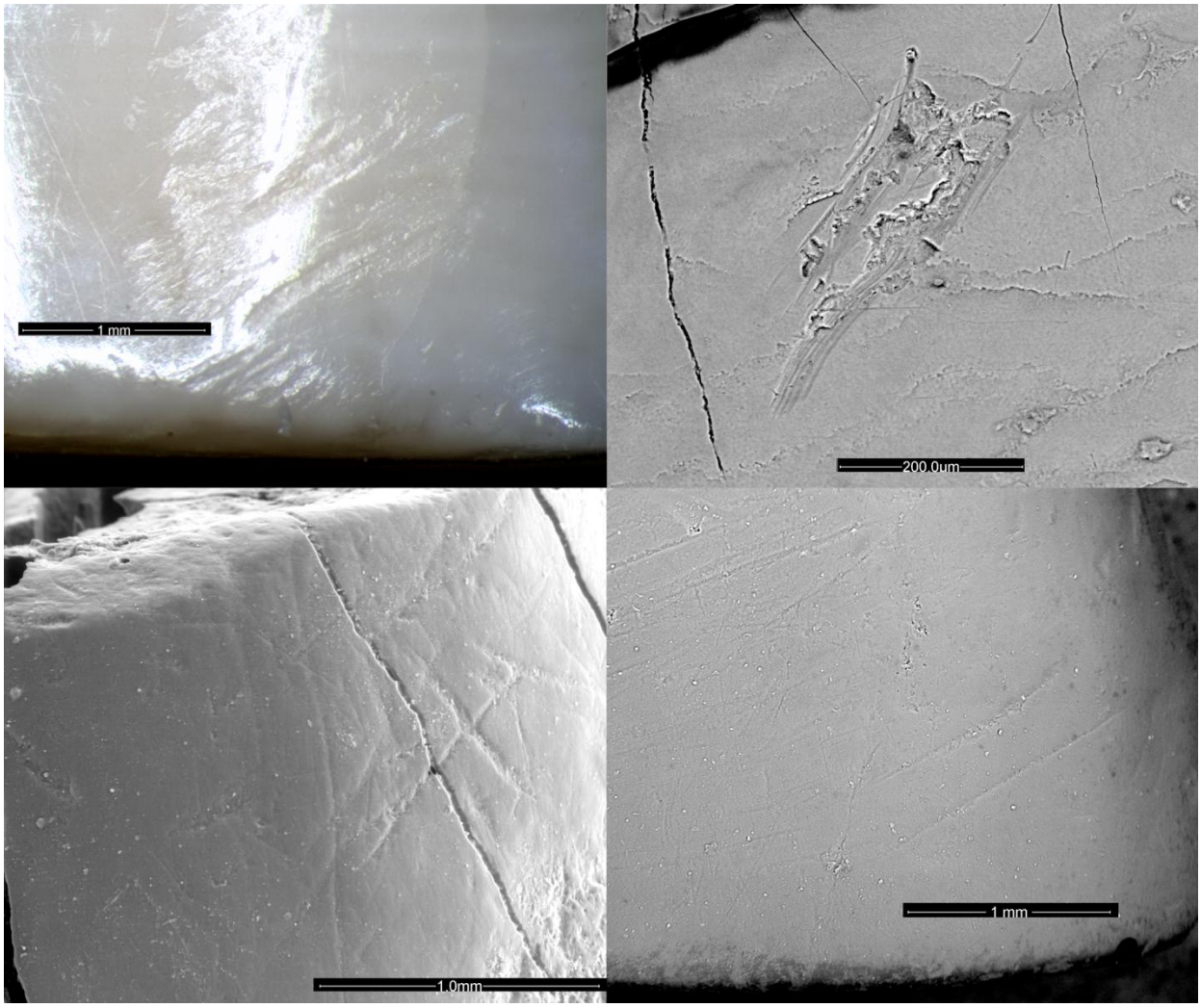


Figure 4

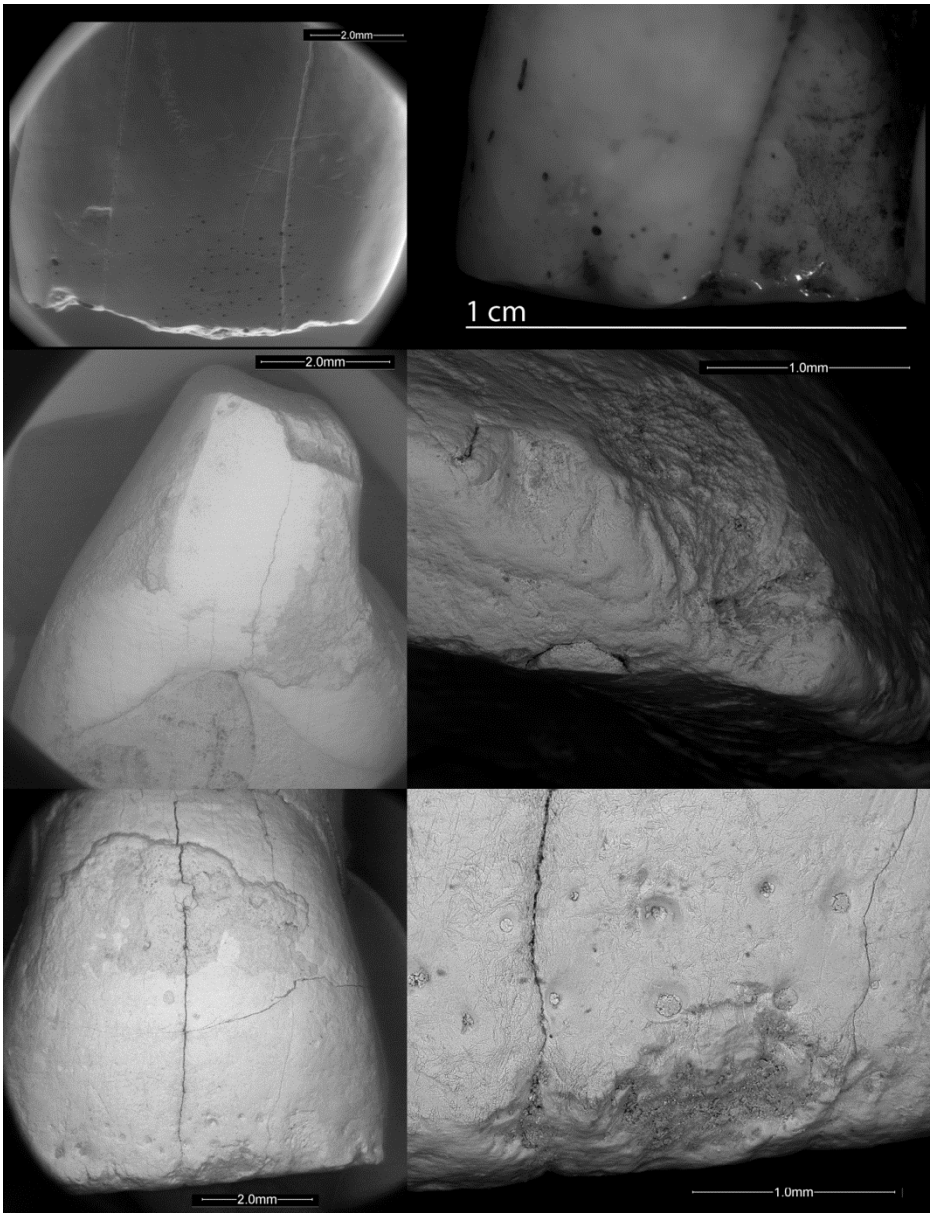
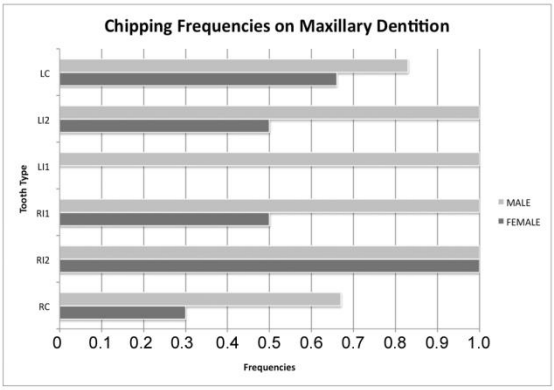
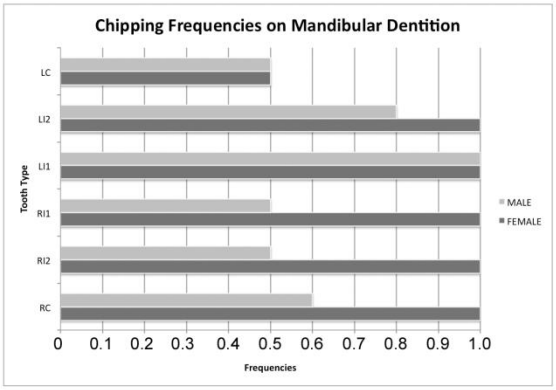
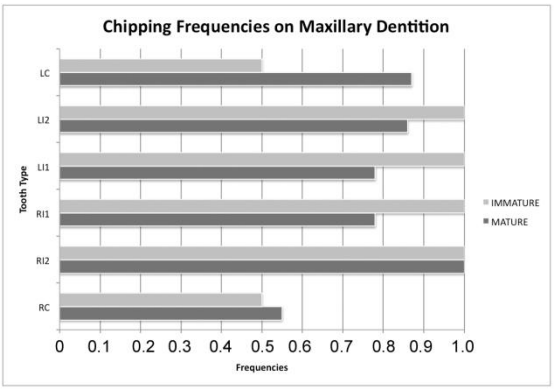


Figure 5


Chipping Frequencies on Maxillary Dentition
Tooth Type
LC
LI2
LI1
RI1
RI2
RC
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Frequencies
MALE
FEMALE


Chipping Frequencies on Mandibular Dentition
Tooth Type
LC
LI2
LI1
RI1
RI2
RC
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Frequencies
MALE
FEMALE


Chipping Frequencies on Maxillary Dentition
Tooth Type
LC
LI2
LI1
RI1
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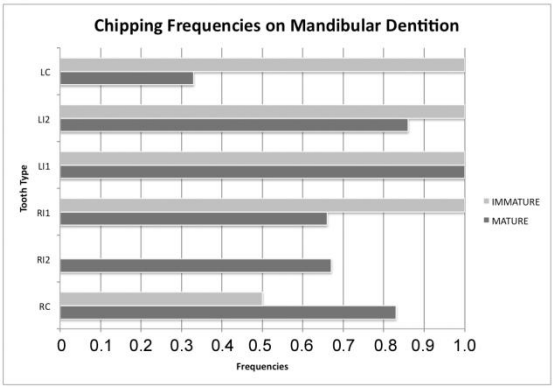
RC
0 0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Frequencies
IMMATURE
MATURE


Chipping Frequencies on Mandibular Dentition
Tooth Type
LC
LI2
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Frequencies
IMMATURE
MATURE

CAPÍTULO VII - LA DIETA DE UN GRUPO NEANDERTAL

Los resultados de este estudio se recogen en las siguientes publicaciones:

Hardy, K., Buckley, S., Collins, M. J., Estalrrich, A., Brothwell, D., Copeland, L., García-Tabernero, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaría, D., Madella, M., Wilson, J., Cortés, A. F., Rosas, A., 2012. Neanderthal medics? Evidence of food, cooking, and medicinal plants entrapped in dental calculus. Naturwissenschaften. 99, 617-26.

Estalrrich, A., Rosas, A., (manuscrito enviado). Diet of a Neandertal Group: Occlusal Molar Microwear Texture Analysis of the El Sidrón (Asturias, Spain). Journal of Human Evolution.

La dieta es uno de los factores que más condiciona las diferencias etológicas y ecológicas entre los primates, determinando el tamaño del grupo y su composición, hábitat y patrones de actividad (Clutton-Brock y Harvey, 1977; Ungar, 1998; Fleagle, 1999).

A la hora de estudiar la dieta de especie extintas, ésta tiene que inferirse a partir de datos indirectos, como ha sido el caso para *Homo neanderthalensis*.

Como se ha comentado en el capítulo anterior, el estudio del registro fósil del Paleolítico medio ha permitido conocer que los Neandertales eran cazadores activos de presas de tamaño grande y medio, que consumían alimentos de origen marino, tubérculos, diversos vegetales y cocinaban su comida (Hoffecker y Cleghorn, 2000; Patou-Matis, 2000; Richards et al., 2000; Gaudzinski y Roebroeks, 2000; Bar-Yosef, 2004; Bocheners et al., 2005; Stringer et al., 2008; Henry et al., 2010; El Zaatari et al., 2011; Fiorenza et al., 2011; Blasco et al., 2012; Hardy et al., 2012; Pinilla et al., 2012; Salazar-García et al., 2013; Henry et al., 2014). Además se han encontrado datos que avalan que los Neandertales que habitaban en ambientes abiertos consumían más carne que los que vivían en ambientes boscosos (El Zaatari et al., 2011; Fiorenza et al., 2011; Pinilla et al., 2012), implicando que el consumo de productos vegetales incrementa según incrementa la cobertura vegetal y la disponibilidad de este tipo de recursos alimenticios.

En este capítulo de la tesis se ha estudiado la dieta de los individuos adultos del yacimiento de El Sidrón, y se ha explorado la diversidad trófica en el grupo Neandertal de la Cueva de El Sidrón y su relevancia ecológica. Hay que mencionar que esta es la primera vez que se estudia la dieta de un grupo Neandertal que tienen relación de parentesco (Lalueza-Fox et al., 2011).

Para ello, se ha analizado el sarro dental y el microdesgaste dental en la cara oclusal de los molares de estos individuos, que se ha comparado con los datos publicados para otros individuos y especies. Además, se ha estudiado la

variabilidad del microdesgaste entre los individuos según el sexo y se ha comparado con la distribución en grupos de cazadores-recolectores actuales agrupados del mismo modo, entre ellos, las muestras aquí analizadas de los individuos del nivel Magdaleniense de la Cueva de la Paloma (Soto de la Regueras, Asturias) y la colección Indian Knoll (Green River, Ohio County, Kentucky, EEUU) adscrito al periodo Arcaico.

VII.1 Metodología

Para el estudio del cálculo dental se ha extraído muestra directamente de los dientes o bien de los moldes, que se ha conservado en tubos Ependorff y posteriormente se ha centrifugado y analizado su contenido.

Por su parte, el análisis de la textura del microdesgaste en la cara oclusal del esmalte dental (MTA, del inglés *dental Microwear Texture Analysis*) se basa en las medidas de la superficie oclusal en 3 dimensiones mediante un microscopio confocal de luz blanca y el análisis fractal (dependiente de la escala) de esa superficie (Ungar et al., 2003; Scott et al., 2005, 2006). Los parámetros o variables que se miden en la superficie dental permiten la caracterización de la superficie de una manera cuantificable, repetible y sin error inter-observador. Esta metodología es una herramienta muy útil para detectar incluso pequeñas diferencias a nivel de individuo (Ungar, 2009; Merceron et al., 2010; Scott et al., 2012). Para la adquisición de los datos de la textura de la superficie oclusal se han realizado réplicas de alta resolución de los dientes, siguiendo los procedimientos previos.

Las réplicas fueron examinadas con un Sensofar Plμ Confocal Imaging Profiler (Solarius Development Inc.) en el Departamento de Antropología de la Universidad de Arkansas.

Después, los datos adquiridos de la superficie fueron analizados mediante el software Toothfrax (Surfract, www.surfract.com) y SFrax usando el análisis fractal (en inglés, SSFA: *Scale-sensitive fractal analysis*).

Las 5 variables generadas son:

Complejidad (Asfc, del inglés *Complexity or area-scale fractal complexity*): mide el cambio en la rugosidad de la superficie a diferentes escalas. Los agujeros y microestrías de diferentes formas y tamaños que se superponen unas sobre otras darán valores altos en estas variable.

Escala de máxima complejidad (Smc, del inglés *Scale of maximum complexity*): mide el límite, en una escala muy pequeña, de la parte más empinada de la curva descrita por la medida Asfc. Las superficies que están dominadas por grandes agujeros y ausencia de estrías, o rasgos aún mayores a grandes escalas, tendrán valores altos de Smc.

Anisotropía (epLsar, del inglés *Anisotropy*): mide el grado de direccionalidad de la rugosidad de la superficie a pequeña escala. Las superficies dominadas por estrías orientadas en la misma dirección tiene valores altos de epLsar.

Volumen de llenado de la textura (Tfv, del inglés *Textural fill volume*): examina el volumen total de cubos de 8 μm^3 (2 μm de lado) que son necesarios para rellenar la superficie. Esta variable depende de la forma de la superficie, y de la textura de la superficie. A una escala grande, una faceta cóncava o convexa tendría un valor

mayor de Tfv que una superficie plana, aunque la textura de ambas fuera la misma. Por eso, al seleccionar un volumen de llenado de cubos de 2 μm de lado, se elimina la estructura general de la superficie, y se caracterizan los datos de la textura propiamente dicha. Una superficie que contenga más rasgos en la escala media, tendrá valores elevados de Tfv.

Heterogeneidad (HAsfc, del inglés *Heterogeneity of complexity or heterogeneity of area-scale fractal complexity*): refleja la variabilidad de la complejidad a lo largo de la superficie. Superficies más heterogéneas (valores altos de HAsfc) tiene una gran variabilidad en la textura, más mezcla de rasgos. Esta variable se ha calculado siguiendo la metodología de El Zaatari (2010) y El Zaatari et al., (2011).

VII.2 Resultados: Caracterización de la dieta del grupo de El Sidrón.

Los resultados del análisis del cálculo dental han mostrado que todos los individuos analizados presentan restos de almidón, indicando que comieron vegetales.

El Sidrón Adulto 2 tiene además restos de bitumen y de haber comido alimentos cocinados. El Sidrón Adulto 3 y Adulto 4 tienen también restos de haber comido alimentos cocinados, y El Sidrón Adulto 3 además presenta restos de camomila o aquilea.

En cuanto al análisis de la microtextura del esmalte, primero se han comparado las variables Asfc (complejidad) y epLsar (anisotropía) entre el grupo de El Sidrón y los Neandertales procedentes de diferentes estudios (El

Zaatari et al., 2011; Hlusko et al., 2013) agrupados según el ecosistema en el que vivieron. También se han incluido en esta comparación dos especies actuales cuya dieta es estrictamente herbívora [*Gorilla gorilla* y *Gorilla beringuei* (Scott et al., 2012)] y dos especies estrictamente carnívoras [*Lycaon pictus* y *Canis latrans* (Ungar et al., 2010)]. Estas dos variables han resultado ser las más efectivas a la hora de distinguir la dieta entre diferentes especies e individuos (Scott et al., 2005; Donohue et al., 2013).

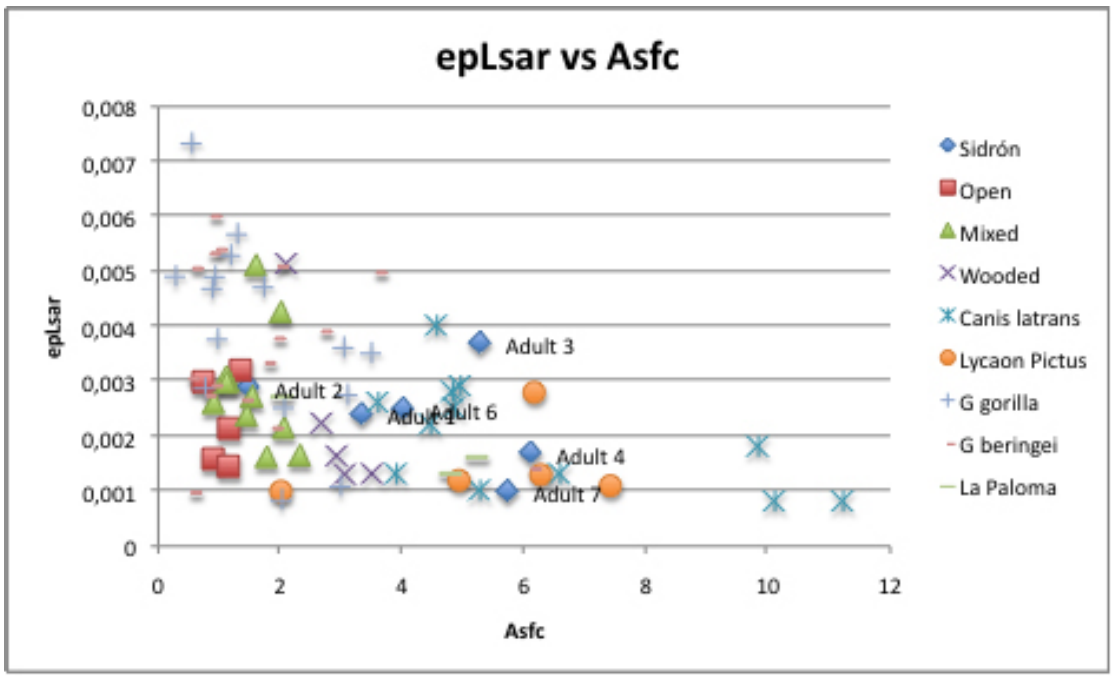

Figura VII.1: Gráfico que muestra las variables complejidad (Asfc) y anisotropía (epLsar) de la muestra analizada y los especímenes usados como modelos de comparación.

Los resultados indican que los individuos del grupo de El Sidrón tienen una alta variabilidad en cuanto a la complejidad de la textura de la superficie oclusal de sus dientes. También indica que estos individuos consumieron más carne (valores más próximos a las especies estrictamente carnívoras) que los Neandertales de ambientes similares (Wooded).

A continuación se ha analizado la variabilidad intra-gurpal (se ha considerado el sexo de los individuos como variable codificante o factor) de la textura del esmalte en El Sidrón, y se ha comparado con la variabilidad de la textura del esmalte dental en los grupos de cazadores recolectores de Indian Knoll (esta tesis), Ipiutak y Tigara (El Zaatari, 2014) y Andamaneses (El Zaatari, 2010). Como los datos no siguen una distribución normal (Scott et al., 2005, 2006) se ha trabajado con estadística no paramétrica. Para la muestra de El Sidrón, dado su pequeño tamaño (N=5) se ha empleado el test de Mann-Whitney U que es el equivalente no paramétrico de T-test (StatSoft Inc, 2013). En los grupos de cazadores recolectores, al tratarse de muestras de mayor tamaño, se ha realizado un test ANOVA de un factor (sexo). Los datos se han transformado previamente en rangos para evitar infringir los supuestos que rigen la estadística paramética (Conover e Iman, 1981).

Los resultados del test de Mann-Whitney U no revela ninguna diferencia significativa en el grupo de El Sidrón, ni tampoco los test ANOVA para los 4 grupos de cazadores-recolectores.

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ORIGINAL PAPER

Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus

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Abstract Neanderthals disappeared sometime between 30,000 and 24,000 years ago. Until recently, Neanderthals were understood to have been predominantly meat-eaters; however, a growing body of evidence suggests their diet also included plants. We present the results of a study, in which sequential thermal desorption-gas chromatography-mass spectrometry (TD-GC-MS) and pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS) were combined with morphological analysis of plant microfossils, to identify material entrapped in dental calculus from five Neanderthal individuals from the north Spanish site of El Sidrón. Our results provide the first molecular evidence for inhalation of wood-fire smoke and bitumen or oil shale and ingestion of a range of cooked plant foods. We also offer the first evidence for the use of medicinal plants by a Neanderthal individual. The varied use of plants that we have identified suggests that the Neanderthal occupants of El Sidrón had a sophisticated knowledge of their natural surroundings which included the ability to select and use certain plants.

Keywords Neanderthals · El Sidrón · Dental calculus · Diet · Self-medication

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Introduction

Neanderthals disappeared sometime between 30,000–24,000 years ago (Finlayson et al. 2006), and little is known in detail about the way in which they lived. Large numbers of animal bones found in association with Neanderthal artefacts led to the assumption that they were predominantly meat-eaters (Burke 2000). This view has been reinforced by stable isotope analyses as the $\delta^{15}N$ values of Neanderthal bone collagen are consistent with a meat-rich diet (Richards and Trinkaus 2009). Most isotope studies are from temperate Europe since few sites in warmer regions have sufficient collagen surviving for analysis, but a $\delta^{15}N$ value recently obtained from El Sidrón, northern Spain, is consistent with earlier findings (Wood et al. 2012).

The similarity of isotopic results across both open and forested environments has led to the suggestion that dietary rigidity may have put Neanderthals at a disadvantage in competition with modern humans (Bocherens 2009); however, there is an increasing range of evidence for greater dietary breadth. The recent identification of the *TAS2R38* bitter taste perception gene in a Neanderthal individual from El Sidrón (Lalueza-Fox et al. 2009) is an indicator of an ability to include plants in the diet as bitterness can warn of toxins (Miller 2011). The survival of actual plant remains within Neanderthal sites is rare; however, evidence for edible grass seeds at Amud Cave, Israel (Madella et al. 2002), charred legumes at Kebara Cave, Israel (Lev et al. 2005), and charred nuts at Gorham's Cave, Gibralter (Barton 2000) suggest these were eaten. Starch granules found embedded in dental calculus from one Neanderthal individual from the site of Shanidar in Iraq and two individuals from Spy in Belgium (Henry et al. 2011) also suggests a plant component in the diet. Furthermore, based on a comparison with the use of similar items from ethnographic contexts, Sandgathe and Hayden (2003) suggest that pointed artefacts of bone and wood found on several Neanderthal sites may have been used to obtain edible inner bark.

Although a buccal molar microwear study has suggested a largely carnivorous diet for the Neanderthals of Gorham's Cave (Lalueza and Pérez-Pérez 1993), a broader survey argues for a mixed diet of animals and plants, with a possible focus on more fibrous plants such as roots and bulbs in cooler periods (Pérez-Pérez et al. 2003). A comparison of occlusal molar microwear patterns including one sample from El Sidrón (SDR-005) suggests a higher consumption of plants in more wooded environments (El Zaatari et al. 2011).

From a broader evolutionary perspective, human saliva contains a substantially higher number of *AMY1* copy variants of the enzyme α-amylase than most other higher primates. The primary role of α-amylase is to break down starch molecules into accessible sugars. As the main constituent of cereal grains, plant storage roots and tubers, many nuts and some inner bark, starch offers the most direct dietary source of glucose, the essential provider of metabolic energy. It has been suggested that the increase in *AMY1* copy variants may have developed as a result of a dietary shift to starchy tubers by early hominins (Perry et al. 2007).

One outcome of an increase in sugar ingestion is the development of dental plaque, formed by the activity of bacteria which are energised by sugars. If dental plaque is not removed, it can calcify within 2 weeks, although accumulation rates are individually variable (Lieverse 1999). Dental calculus has a rough surface that provides an ideal location for further microbial activity, leading to increased plaque development in which the calculus appears to accumulate in layers (Hardy et al. 2012). Calculus is found on both the labial and lingual sides of the tooth and can occur above or below the gum, where it is known as supra- or subgingival calculus, respectively. Dental calculus adheres strongly to the tooth, it has been found on the teeth of hominids dating to 1.8 million years (Blumenschine et al. 2003). Most of the research on archaeological samples of dental calculus has focused upon the extraction and identification of plant microfossils (Piperno and Dillehay 2008; Hardy et al. 2009; 2012; Charlier et al. 2010; Henry et al. 2011), but a recent study successfully extracted sufficient protein for stable carbon and nitrogen isotope analysis (Scott and Poulson 2012).

In this study, we present new results obtained from the dental calculus of five Neanderthal individuals using sequential thermal desorption-gas chromatography-mass spectrometry (TD-GC-MS) and pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS). The combination of these techniques enables the identification of both free/unbound and bound/polymeric organic components (Buckley et al. 1999). By using these methods in conjunction with the extraction and analysis of plant microfossils, we have found chemical evidence consistent with wood-fire smoke, a range of cooked starchy foods, two plants known today for their medicinal qualities, and bitumen or oil shale entrapped within the dental calculus. Yet within the same calculus, chemical evidence for lipids/proteins from meat was low to absent.

Materials and methods

El Sidrón Cave is located in Asturias in Northern Spain, 15–20 km from the modern coastline. Approximately 2,000 skeletal remains representing at least 13 Neanderthal individuals have been found, aged between 47,300 and 50,600 BP (de Torres et al. 2010; Wood et al. 2012; Rosas 2012). The total dental sample comprises 184 specimens, belonging to a minimum of 13 individuals both adult and juvenile. All the El Sidrón individuals have dental calculus. Deposits range from small (grade 1–2, [Hillson 2001]), particularly in the case of the juveniles, to medium (grade 3) and

large (grade 4) for the adults (Rosas et al. 2006), suggesting that the calculus was cumulative and covers an extended period of the individuals' lives. Over 76 % (39 teeth) of the premolars and molars also have sub-vertical grooves; the cause of these is unclear but may be linked to erosion by particles ingested with food (Estalrrich et al. 2011).

Ten samples of dental calculus from five Neanderthal individuals were analyzed in this study. Each individual is identified by its overall age status (adult, adolescent or juvenile) followed by a number (1, 2, 3, etc.). Each dental calculus sample is identified by the letters SD or SDR, followed by a unique identifying code (Rosas et al. 2006). Four samples are from the Neanderthal individual catalogued as Adult 2 (SD-1427m upper right M^1, SD-1427b upper left M^3, SD-1427c upper left M^2, SDR-007c lower left P^2), two samples from Adult 3 (SD-1217e lower left M^1, SD-1218a lower left M^2), one sample from Adult 4 (SD-1604 upper left M^2), two samples from Adult 5 (SD-1327i lower left M^2, SD-1327 h lower left M^1), and one sample from Juvenile 1 (SD-1716 lower right I^2) (Table 1). The variable number of samples from each individual is due to the differential presence of calculus.

Although the sample size varied, no sample was larger than 2×1 mm. Three of the largest samples were split into two (Adult 2 SDR-007c, Adult 2 SD-1427c, Adult 4 SD-1604), and in one case (Adult 3 SD-1217e) three parts for multiple analysis. In order to record bacteria, scanning electron microscopy, using 0.5–1 mm^2 samples was conducted on two samples (Adult 2 SD-1427c, Adult 3-1217e), while TD-GC-MS and Py-GC-MS was conducted on three samples (Adult 2 SDR-007c, Adult 3 SD-1217e, Adult 4 SD-1604). A minimum size of 0.7 mg was required to conduct TD-GC-MS and Py-GC-MS. Extraction and optical microscopy of plant microfossils was conducted on all samples.

Samples were collected on two separate occasions. The first batch of samples were retrieved in December 2009; this included two samples of dental calculus which were accidentally dislodged during cleaning of the mandibles (Adult 2 SD-1427m, Adult 2 SD-1427b,) and a further three samples (Adult 3 SD-1218a, Adult 3 SD-1217e, Adult 5 SD-1327i), which had adhered to the moulds made of the mandibles. In this case, the relevant parts of the moulds were cut out, placed in closed centrifuge tubes, and sonicated until the material dislodged (~6 min.). The samples which were dislodged during cleaning have only been used for extraction of plant microfossils and do not contribute to the detailed results. A further five samples (Adult 2 SDR-007c, Adult 2 SD-1427c, Adult 4 SD-1604, Adult 5 SD-1327h, Juvenile 1 SD-1716) were removed from the teeth in May 2010. These samples were prised off with a scalpel, dropped onto aluminium foil then retrieved immediately using tweezers and placed into Eppendorf tubes. All this work was undertaken in the El Sidrón laboratory at the Museum of Natural History, Madrid, except the sonication which took place in BioArCh, University of York. Under ideal circumstances, soil samples adjacent to the calculus would also be available for analysis.

Table 1 Dental calculus material sampled

Individual	Sample number	Mitochondrial lineage (Lalueza-Fox et al. 2011)	Tooth	Calculus location	SEM	TD-GC-MS and Py-GC-MS	Micro-fossils
Adult 2 Young male	SD 1427m	A	Upper right M^1	Unknown (dislodged during cleaning)			X
Adult 2 Young male	SD 1427b	A	Upper left M^3	Unknown (dislodged during cleaning)			X
Adult 2 Young male	SD 1427c	A	Upper left M^2	Lingual supra gingival	X		X
Adult 2 Young male	SDR 007c	A	Lower left P^2	Lingual supra gingival	X	X	X
Adult 3 Female	SD 1217e	B	Lower left M^1	Removed from mould	X	X	X
Adult 3 Female	SD 1218a	B	Lower left M^2	Removed from mould			X
Adult 4 Young adult female	SD 1604	C	Upper left M^2	Lingual supra/sub gingival (mixed)		X	
Adult 5 Female	SD 1327i	A	Lower left M^2	Removed from mould			X
Adult 5 Female	SD 1327h	A	Lower left M^1	Lingual supra gingival			X
Juvenile 1 5–6 years	SD 1716	C	Lower right I^2	Labial supra gingival			X

Scanning electron microscopy (JSM-6490) of two samples (SD-1427c, SD-1217e) coated with 15–20 nm gold-palladium was undertaken at 20,000-fold magnification. Three samples of dental calculus from three separate individuals (Adult 2 SD-1427c, Adult 3 SD-1217e, Adult 4 SD-1604) were analyzed by TD-GC-MS and Py-GC-MS using a CDS Pyroprobe 1000. Samples were thermally desorbed at 310 °C for 10 s in open split mode at 30ml/min. Initially, the GC was held at 35 °C for 5 min, then temperature was programmed from 40–340 °C at 6 °C per minute and held at final temperature for 15 min, total 65 min. The run was repeated with the same sample being pyrolysed at 610 °C for 10 s. Four control samples of dental calculus including a modern (Hoy) sheep and an (Alsatian) dog, and two samples from the Victorian cemetery of St Barnabas, London were used for comparative purposes to assist in the interpretation of the El Sidrón material (ESM_1.pdf). Plant microfossils extraction was conducted on all samples according to a standard method (Hardy et al. 2009) in which samples were first rinsed in 0.6 M HCl for 5 min to remove adhered surface carbonates. They were then dried and coarsely ground. The resulting powder was suspended in 1.5 ml of 0.6 M HCl, vortexed every 15 min for 1 h, then centrifuged at room temperature at 13,000 rpm for 15 min. Samples were viewed on an Olympus IX 71 inverted microscope. Imaging was conducted using a Colour View camera and Cell D imaging system.

Results

Table 2 summarizes the material observed and identified from the dental calculus samples.

Adult 2—SDR-007c (lower left P^2)

The thermal desorption-GC-MS (TIC) (Fig. 1 inset) is dominated by a series of *n*-alkanes (carbon numbers C22 to C35), suggesting a higher plant source (Eglinton et al. 1962), most probably derived from plant waxes in the original food consumed. Also identified were a series of hopanes (carbon numbers C29 to C33), indicative of an oil shale or bitumen and corroborated by the presence of the isoprenoid hydrocarbon biomarkers phytane and pristane (Williams and Douglas 1986; Connan 1999). The pyrolysis-GC-MS (TIC) (Fig. 1) was dominated by C4 to C30 *n*-1-alkenes and *n*-alkanes, typical of unsaturated and saturated fat/oil-derived acyl lipids

Table 2 Results of scanning electron microscopy, TD-GC-MS and Py-GC-MS and microfossil extraction from dental calculus samples

Sample no.	SEM analysis	MS Markers	Microfossils	Interpretation
Adult 2				
SD-1427m	NA	NA	9 starch	Ate starchy food
SD-1427b	NA	NA	>20 starch 1 phytolith	Ate starchy food
SD-1427c	Filamentous and coccoidal.	NA	8 starch	Ate starchy food
SDR-007c	NA	HC, FAME, C, PAH, Ho, Ph Pr	20 starch	Ate several different cooked starchy plants. Inhaled woody smoke. No evidence for protein, Evidence of contact with oil shale/bitumen.
Adult 3.				
SD-1217e	Filamentous and coccoidal.	HC (trace)	8 starch	Ate cooked starchy food
SD-1218a	NA	NA	7 starch	Ate starchy food
Adult 4				
SD-1604	NA	HC, C, PhOH, PA, PAH, Az, Co, Ac*	0 starch	Ate a range of cooked carbohydrates. Azulenes and coumarins consistent with yarrow and camomile. Inhaled wood smoke and/or ate smoked food. Protein markers. No evidence of lipids from animal meat. Traces of moulding material.
Adult 5				
SD-1327i	NA	NA	5 starch	Ate starchy food
SD-1327 h	NA	NA	8 starch	Ate starchy food
Juvenile 1				
SD-1716			4 starch	Ate starchy food

Key to abbreviations: *HC* hydrocarbon, *FAME* fatty acid methyl ester, *C*=2-cyclopenten-1-one derivatives, *PAH* polynuclear aromatic hydrocarbons, *Ho* hopanes, *Ph* phytane, *Pr* pristane, *PhOH* phenols, *PA* phenolic acids, *Az* azulenes, *Co* coumarins, *Ac** acrylates *modern contamination (for details on chemical compounds, see ESM_4 pdf)

and higher plant waxes (Buckley et al. 1999). Thermally derived carbohydrate markers (2-methyl-2-cyclopenten-1-one and 2,3-dimethyl-2-cyclopenten-1-one) were also identified (McCobb et al. 2001). The absence of these compounds in the TD profile provides molecular evidence for a polymeric carbohydrate source, consistent with a starchy plant. The presence of 20 starch granules in this sample confirms this finding and demonstrates the ingestion of starchy material. Although it is not possible to identify the exact plant source of these starch granules solely on the basis of their morphology (Wilson et al. 2010), their small size and angular nature suggests a seed source rather than a tuber; granules that grow in a compact environment such as a seed case tend to develop angularly, while granules growing in a less-restricted environment such as a tuber are more likely to have smooth edges. The presence of the fatty acid methyl esters, methyl palmitate, and methyl stearate can suggest methylation of the fat/oil triglycerides at high temperature, i.e., cooking. Although fatty acid methyl esters have been previously observed as minor components of fungal spores and bacteria (Laseter et al. 1968; Maudinas and Villoutreix 1977), their molecular composition is very different. In contrast, these methyl esters would be expected to be the main fatty acid methyl esters formed from the heating of lipids, i.e., fats. The additional presence of the main combustion markers, fluorathene, and pyrene, along with smaller amounts of fluorene and phenanthrene, strongly supports the evidence for cooking/smoke inhalation in this sample (Ré-Poppi and Santiago-Silva 2002; Varlet et al. 2006). It is notable and highly relevant that the relative abundances of these combustion markers are entirely consistent with those found in wood smoke (Rogge et al. 1998; Seng et al. 2007). No free bacterially derived components such as branched acyl lipids and hydrogenated steroids were observed, nor any bacterially derived hydrocarbons originating from the branched fatty acid acyl groups (significant components of bacterial triglycerides) were observed in the TD/Py-GC-MS of this sample (Shorland 1962). This suggests that the components in the dental calculus derive from the diet, yet notably, there were no diagnostic protein markers or steroidal compounds indicative of meat ingestion.

Adult 3—SD1217e (lower left M¹)

The thermal desorption-gas chromatography-mass spectrometry (TD-GC-MS) total ion chromatogram (TIC) revealed no detectable components, indicating the absence of any free, thermally extractable lipids in this sample. The pyrolysis-gas chromatography-mass spectrometry (Py-GC-MS) TIC identified very few components, with only low molecular weight aromatic hydrocarbons and alkenes of uncertain origin detected. This absence of significant markers suggests that micro-organisms that form the

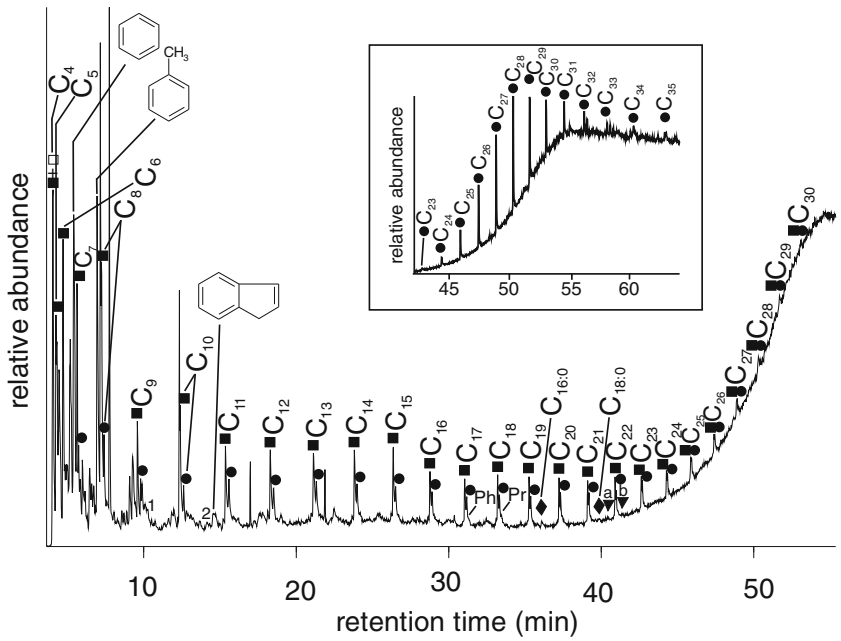

Fig. 1 Reconstructed total ion chromatogram of the pyrogram (pyrolysis profile) (610 °C for 10) of sample SDR-007c, after thermal desorption (310 °C for 10 s). Key to Fig. 1: Peak identities (*x* indicates carbon chain length): *filled diamonds*, Cx:0 indicates saturated fatty acid methyl esters; *filled squares*, Cx indicates alkenes; *filled circles*, Cx indicates alkanes; *inverted triangles*, *a* is fluorathene and *b* is pyrene. Ph is phytane and Pr is pristane. Peak 1 is 2-methyl-2-cyclopenten-1-one and 2 is 2,3-dimethyl-2-cyclopentene-1-one. Also shown are the structures of three aromatic compounds identified: benzene, toluene, and indene. *Inset* displays a reconstructed total ion chromatogram of the thermal desorption profile (310 °C for 10 s) of this sample. Peak identities: *filled circles*, Cx indicates alkanes

calculus do not contribute significantly to the overall organic signal. All the other samples (SD-1427b, SD-1427c, SD-1427, SD-1218, SD-1716, SD-1327i) had evidence for the consumption of starchy food in the form of actual starch granules. Furthermore, the basal part of a trichome phytolith compatible with grass plants (Poaceae) (Kaplan et al. 1992) was recovered in sample SD-1427b. The phytolith was broken towards the edge and the hair tip was missing. Starch is concentrated in grass seeds, and this can be accessed relatively easily by chewing, although we did not observe any of the grass-like starch granules reported by Henry et al. (2011).

Adult 4—SD1604 (upper left M²)

A range of alkyl phenols and polynuclear aromatic hydrocarbons (PAHs) suggest the ingestion of wood smoke or smoked foods by this individual (Ré-Poppi and Santiago-Silva 2002; Varlet et al. 2006). Recent studies of modern cigarette smokers suggests that smoking increases the development of calculus (Bergström 1999, 2005), though it is not possible at present to determine whether smoke inhalation had an effect on the quantity of dental calculus found on the Neanderthal teeth. A range of carbohydrate compounds greater than that observed in SDR-007c suggests the possibility of several different nutritional plants, with this sample being particularly notable for the presence of azulene and coumarin derivatives. The former includes azulene, dihydroazulene, 4,6,8-trimethylazulene and chamazulene (7-ethyl-1,4-dimethylazulene), and the latter 4,5,7-trimethylcoumarin, 4-methylherniarin (7-methoxy-4-methylcoumarin), and the tentatively identified scopoletin (6-methoxy-7-hydroxycoumarin). The presence of chamazulene, dihydroazulene, and 4-methylherniarin is also notable since the two former compounds, together with herniarin, occur in yarrow (*Achillea millefolium*), and chamazulene and herniarin in camomile (*Matricaria chamomilla*). Also significant pyrolysis components of the organic material within the calculus were the thermolytically derived methyl esters of the aromatic acids 4-hydroxyphenylacetic acid and 3-hydroxyphenylacetic acid, together with their methoxy-derivatives (McCobb et al. 2001). These, and similar phenolic acids, occur in a number of food sources including nuts (Senter et al. 1983). Toluene and *o*-, *m*-, and *p*-xylenes in moderate abundance, while lower abundances of pyridine, pyridine, 2-methyl pyridine, 3-methyl pyridine, 4-methyl pyridine and pyrrole were present; these are indicative of the consumption of protein. Notably, however, the absence of any lipid components in the dental calculus means that this individual has no evidence of fat consumption, as would be expected in a meat-based diet. Traces of the material used to make moulds of the mandibles were also found. The pyrogram displayed a number of carbohydrate markers, in addition to those detected in SDR-007c, suggesting a more complex range of carbohydrates was present. Protein markers were also present but protein–lipid condensation products (e.g., aliphatic nitriles and amides) were absent, suggesting the absence of a significant amount of lipid in this sample. No starch granules were detected in this sample, which may simply be a product of sampling, as carbohydrate markers were found (see above). A possible indication of pyrolyzed lutein was also detected; this is a xanthophyll (yellow pigment) commonly found in green vegetables. The combined presence of the alkyl phenols and polynuclear aromatic hydrocarbons (PAHs) has been observed in wood smoke and smoked foods (Ré-Poppi and Santiago-Silva 2002; Varlet et al. 2006), their presence in the calculus suggesting proximity to a fire, and/or the ingestion of cooked or smoked food. Other significant pyrolysis components detected are also known to occur in a number of other food sources, including nuts (Senter et al. 1983; McCobb et al. 2001) (See ESM_2pdf for detailed results).

Starch granules

Starch granules were found in nine of the ten samples (Table 2, ESM_3.pdf). While there is always a potential risk of contamination, starch granules were recorded embedded in the dental calculus matrix, eliminating the possibility that these could be recent contaminants (Fig. 2a). Starch is identified initially through its size, shape, and birefringence. The birefringence is caused by the ordered arrangement of the component

Fig. 2 Microscopically visible material entrapped in dental calculus samples. **a** Group of starch granules still embedded in dental calculus matrix (SD 1427b). **b** Damaged starch granule (17 um diameter) viewed under polarized light. Note the cracking around the exterior caused by damage or degradation of the granule (SD 1327i). **c** Filamentous and cocci bacteria (sample SD 1427c)

amylose and amylopectin polymers, which produces a characteristic "Maltese Cross" interference pattern when viewed under cross-polarized light. Other materials, including water bubbles, can however produce a similar effect (Hardy et al. 2009). To confirm that the material observed microscopically is indeed starch (*Bacillus licheniformis*), alpha-amylase (0.25 ml of undiluted 1, 4-alpha-D-glucan-glucanohydrolase) was dropped onto a sample of granules and incubated at 25 °C for 24 h. Positive and negative controls (modern starch with and without amylase) were also used. Since all the positive control samples and archaeological granules disappeared while the negative control sample survived, we therefore conclude that the granules were composed of starch. The different sizes and shapes present in the samples suggest the possibility of more than one plant genus. This is also consistent with the mass spectrometry results which suggest a range of carbohydrate sources.

It has been argued that it is difficult to confirm that partially gelatinized starch granules are in fact cooked, as gelatinization would be a stage in the long-term disintegration of the granule (Collins and Copeland 2011). However, if the starch is dry-heated (parching or popping), granules lose water and this can cause cavities (Copeland et al. 2009). Edge cracking, which may be consistent with dry-heat, was observed in several of the starch granules (Fig. 2b). It is not unreasonable to suggest that dry heat produces a hardening of the granule case, which can then result in a resistance to moisture adsorption (Collison 1968) and may assist in long preservation.

Oral health

Fossilized bacteria, both elongated filamentous and, less commonly, coccoidal, were observed by scanning electron microscopy (Fig. 2c). Both morphotypes have been identified in Neanderthal individuals from Subalyuk 2, Kebara 2, and Spy (Vandermeersch et al. 1994; Pap et al. 1995). The proportion of filamentous to cocci type bacteria is similar to that observed in a sample from Subalyuk 2 (N Hungary) but differs from a sample from Kebara 2 in which cocci bacteria were more common (Vandermeersch et al. 1994). The presence of bacteria with different morphologies in all observed samples from El Sidrón, together with those found in the samples from different sites, suggests this is an untapped resource for information on past dental and physical health.

Discussion

Oil shale

In one sample (SDR-007c), traces of a possible oil shale or bitumen were identified by a series of hopanes and the isoprenoid hydrocarbons phytane and pristane. Bitumen is known to have been used as a hafting material by Neanderthals (Boeda et al. 2008), while the nearest oil shale source to El Sidrón is located 15 km east at Llames de Parres (Kruge and Suárez-Ruiz 1991). Although further biomarker work is needed to determine a specific characteristic molecular fingerprint, our findings raise the possibility that this individual may have visited Llames de Parres, or worked with bitumen collected from this site.

Food and medicine?

The principal problem in evaluating the exploitation of plants in pre-agricultural times is the lack of direct evidence; nonetheless, O'Connell et al. (1999) argue that *Homo erectus* had a high dependence on tubers. It has also been argued that the exploitation of starchy roots was a significant factor in the expansion of hominins into a savannah environment (Laden and Wrangham 2005). Although these are theoretical perspectives, they correlate well with the high salivary amylase identified in modern humans in comparison with other higher primates (Perry et al. 2007).

The presence of pigments and bitter-tasting appetite suppressants (dihydroazulene and chamazulene, and the coumarin, 4-methylherniarin) in the calculus of Young Adult 4—SD1604 is intriguing. One possible reason for the consumption of bitter-tasting plants with no nutritional value and containing these compounds (such as yarrow and camomile) would be for self-medication. All the higher primates have a wide and applied knowledge of the edible plants within their environments, and there is an extensive body of evidence demonstrating the complex use of medicinal plants for zoopharmacognosy by animals including all modern higher primates (e.g., Rodriguez and Wrangham 1993; Cousins and Huffman 2002; Huffman 1997, 2003; Singer et al. 2009; Lisonbee et al. 2003; Krief et al. 2005; Huffman and Vitazkova 2007).

The starch granules and carbohydrate markers in these samples, the evidence for the azulene and coumarin compounds, the possible evidence for nuts, grasses, and possibly even green vegetables, argue for a broader use of ingested plants than is often suggested by stable isotope analysis. This view is compounded by the surprisingly low levels of protein markers (in the form of diketopiperazines, DKPs), which were lower than in control samples of modern calculus from dog and sheep (ESM_1.pdf). Though preferential degradation of residual protein was considered, the survival of sufficient levels of collagen in both bones and teeth to undertake racemization and radiocarbon dating (de Torres et al. 2010) suggests that the absence of protein is a genuine indicator of low protein levels in the diet during the period over which the dental calculus accumulated.

The beginnings of cooking are suggested to be as far back as 1.9 Ma (Wrangham et al. 1999); the presence of

hearths and burnt bone on many Neanderthal sites suggests that they cooked at least some of their food. Using mass spectrometry, we have identified the ingestion of cooked carbohydrates in the calculus of two adults, one adult in particular having apparently eaten several different carbohydrate-rich foods. The evidence for cooked carbohydrates is confirmed both by the cracked/roasted starch granules observed microscopically and the molecular evidence for cooking and exposure to wood smoke or smoked food in the form of methyl esters, phenols, and polynuclear aromatic hydrocarbons (notably pyrene and fluoranthene) found in the dental calculus.

Neanderthals lived through different climatic regimes, including periods in which numerous edible plants were available for exploitation (Jones 2009; Hardy 2010; El Zaatari et al. 2011). We propose that that the Neanderthal occupants of El Sidrón, whose hypothesized, cannibalized remains (Rosas et al. 2006) were discarded at the site, had a sophisticated knowledge of their natural surroundings, and were able to recognize both the nutritional and the medicinal value of certain plants. Although the extent of their botanical knowledge and their ability to self-medicate must of course remain open to speculation, the fact that higher primates have some understanding of the flora within their environment, and the extensive evidence for self-medication within the animal kingdom, would surely make it surprising if the Neanderthals did not also share such knowledge.

We believe that our findings offer the first direct molecular evidence for the ingestion of carbonized food and the inhalation of smoke by a Neanderthal individual. We also offer the first measurable molecular evidence that dental calculus is a trap for ingested material, the starch granules reported from El Sidrón representing the oldest granules ever to be confirmed using a biochemical test. Our approach to the study of this material, combining analytical chemistry with morphological observation, offers the opportunity to maximize the biographical detail to be gained for ancient human populations.

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Diet of a Neandertal Group: Occlusal Molar Microwear Texture Analysis of the El Sidrón (Asturias, Spain).

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Key index words

Occlusal Molar Microwear Texture Analysis; *Homo neanderthalensis*; Dietary variability.

Abstract

Variability of the occlusal dental microwear texture in molar teeth of a Neandertal group from the El Sidrón cave (Spain) is explored. We have compared the microwear texture signatures of these samples with the original data from modern *Homo sapiens* groups from the Magdalenian site of Cueva de la Paloma (Spain) and the Indian Knoll collection (USA) from the Archaic Period. Comparisons were also made with data reported by previous authors for Neandertal individuals, five bioarchaeological hunter-gatherer groups from different paleoecological landscapes, and four extant species, two are mainly herbivorous (*Gorilla gorilla* and *G. beringei*), and two are mainly carnivorous (*Canis latrans* and *Lycaon pictus*).

Our results reveal that, in general terms, the El Sidrón group had a mixed diet, and that meat was and important component. When compared with other Neandertals, El Sidrón Neandertals have complexity (Asfc) values higher than the average value of the individuals from the same kind of wooded environment, probably duet to a high intake of abrasive particles on the foods

Despite no statistically significant sex-related differences were found on the on the microwear signatures of the individuals from Cueva de la Paloma, Indian Knoll, and El Sidrón samples, Neandertal adult females from El Sidrón show higher values of Asfc than males from their group, that could be related to non-masticatory dental wear. As the samples have small size, these results must be taken with caution. Interestingly, one individual from El Sidrón group shows an extreme value for the scale of maximum complexity variable that has been related to the mastication of a large abrasive item, although not in a habitual basis.

Introduction

Diet has been recognized as one of the main factors that determine the behavioral and ecological differences among primates, which means that diet influences group size and composition, habitat range, activity patterns, and so on (Clutton-Brock and Harvey, 1977; Ungar, 1998; Fleagle, 1999, among others). The dietary behavior can be directly observed in living primates, but the diet of fossil individuals must be inferred from indirect evidence, as has been the case for *Homo neanderthalensis*.

Based on the study of the Middle Paleolithic (MP) fossil and archaeological records, we now know that Neandertals were active hunters who had a wide food range, exploiting marine food, big to small prey, vegetables and tubers, and who cooked their food (Hoffecker and Cleghorn, 2000; Patou-Matis, 2000; Richards et al., 2000; Gaudzinski and Roebroeks, 2000; Pérez-Pérez et al., 2003; Bar-Yosef, 2004; Bocheners et al., 2005; Stringer et al., 2008; Henry et al., 2010; El Zaatari et al., 2011; Fiorenza et al., 2011; Blasco et al., 2012; Hardy et al., 2012; Pinilla et al., 2012; Salazar-García et al., 2013; Henry et al., 2014; Sistiaga et al., 2014). From all these evidences,

In 2011, El Zaatari and collaborators reconstructed the diets of Neandertals from different temporal and ecogeographical ranges by means of analyzing the occlusal molar microwear textures. They demonstrated that the increase in the levels of heterogeneity (*HAsfc*) and surface complexity (*Asfc*) is correlated with the increase in tree cover, which could reflect an increase in the level of individual dietary variability due to the availability of plant foods. Comparisons with modern hunter-gatherers have shown that the Neandertals from open-steppe environments had a diet consisting almost exclusively of meat, with low inter-individual variability. In addition, Neandertals from mixed environments ate predominantly meat, but also included several plant foods, whereas Neandertals from wooded environments had a mixed diet with higher intakes of plant foods, as compared with the other two Neandertal groups. This dietary diversity has also been supported by the data on dental mesowear by Fiorenza and collaborators (2011), and buccal microwear (Pérez-Pérez et al., 2003; Pinilla et al., 2012). Therefore, Neandertals had a subsistence economy analogous to hunter-gatherers, relying on the prey and plant foods available in the ecosystem in which they lived.

As our ability to know the dietary behavior of this extinct species increases, so increases our curiosity to know what was happening within the Neandertal groups. A better knowledge of the diet distribution among individuals of the same group may help to clarify Neandertal social organization, with implications on demographic patterns. In this study, we analyze the occlusal molar microwear textures to reconstruct the dietary habits of 6 adult individuals from the El Sidrón Neandertal group (Spain), using only those individuals with good preservation of the occlusal molar surfaces. As the occlusal dental microwear texture analysis (MTA) has been demonstrated to be a useful analytical tool to detect subtle differences even at the individual level (Merceron et al., 2010; Scott et al., 2012), we explore the dietary variability within the Neandertal groups based on the age-at-death and sex of the individuals. We

compare these results with modern *Homo sapiens* groups from the Magdalenian site of Cueva de la Paloma (Soto de la Regueras, Asturias, Spain) and the Indian Knoll collection (Green River, Ohio County, Kentucky, USA) from the Archaic Period.

Materials

El Sidrón Cave Neandertals (Spain)

El Sidrón site is located in north-western Spain. Detailed information about the site can be found elsewhere (Fortea et al., 2003, 2008; Rosas et al., 2006; Lalueza-Fox et al., 2011; Rosas et al., 2012, 2013). At the moment, the MNI identified at the site is 13 (Rosas et al., 2013), with a date of approximately 49 kya for the Neandertal fossil assemblage (Wood et al., 2013). The sample studied here comprises the first or second molars from six adult individuals, all them with good preservation of their occlusal surface. The fossils are housed at the Department of Paleobiology at National Museum of Natural Sciences (MNCN-CSIC) in Madrid, Spain. Approximate age-at-death for the individuals (Rosas et al., 2012, 2013) was estimated based on dental development following Alqahtani et al. (2010). Canine odontometrics, mandibular morphology, and presence (or absence) of Y-chromosome markers have been used to assign individual sex (Lalueza-Fox et al., 2011; Rosas et al., 2012). The individuals here considered include two females, three males, and one remains undetermined.

Cueva de la Paloma (Soto de las Regueras, Asturias, Spain)

The site was excavated in 1914-15 (Hernández-Pacheco, 1923; Hoyos et al., 1980). The analysis of artifacts, both lithics and bone industry, suggest that there are nine archaeological levels, of which only three contain human remains: Level 2 is associated to the Azilian culture; and Levels 8 and 9 to the Magdalenian culture (Hernández-Pacheco, 1923; Barandiarán, 1971; Hoyos et al., 1980; Straus, 1992; Meiklejohn, 2009). The human remains are housed at the National Museum of Natural Sciences (MNCN-CSIC), and this is the first time that they are being examined. For this study, we have selected three adult individuals (two females and one male) from the Magdalenian level, all them with a good preservation of the occlusal molar surface

Indian Knoll (Green River, Ohio County, Kentucky, USA)

The Indian Knoll collection belongs to a prehistoric population located on the Green River (Ohio Co.), and dated at 5590–4530 cal yr B.P. (Morey et al., 2002), during the Middle and Late Archaic period. The site was first excavated during 1915 and completed after the Depression (Webb, 1974). The Indian Knoll population is described as fisher-hunter-gatherers, whose diet consisted mainly of meat from deer, but also from small birds and turkey. Mussels were also an important source of proteins (Webb, 1974), as their habitat was a wetland (Morey and Crothers, 1998; Morey et al., 2002). The skeletal remains studied here are located at the Department of Anthropology at the National Museum of Natural History (Smithsonian Institution, Washington D.C.). Demographic

profiles were provided for each individual, based on the study of several authors (Snow et al., 1948; Webb, 1974). The sample here studied comprises 25 adult individuals: 13 males, and 12 females.

Methods

Surface Texture data acquisition

For the study of occlusal molar microwear texture analysis, high-resolution replicas were prepared following conventional procedures. First, all teeth were cleaned with an artist paintbrush soaked with acetone or ethyl alcohol to remove preservatives, and then with distilled water to complete the cleaning. Moulds of the teeth were made using a hydrophilic vinyl polysiloxane resin (Bromage, 1987; Martínez-Maza et al., 2011; Estalrrich and Rosas, 2013) and the replicas were made with epoxy resin (Scott et al., 2006; El Zaatari et al., 2011; Hlusko et al., 2013), following the conventional procedures.

The replicas were then examined using a Sensofar Plμ Confocal Imaging Profiler (Solarius Development Inc.) located at the Department of Anthropology at the University of Arkansas. Four adjoining scans, representing a total area of 276 x 204 μm of the Phase II facet 9 from M1s or M2s were made. These procedures have been described extensively elsewhere (e.g. Ungar et al., 2003; Scott et al., 2005; Scott et al., 2006; Scott et al., 2012). Briefly, the five variables generated are:

Complexity or area-scale fractal complexity (*Asfc*): measures change in surface roughness at different scales. Pits and scratches of different sizes and shapes overlapping one another would present a complex surface, with high complexity values.

Scale of maximum complexity (*Smc*): measures the fine scale limit of the steepest part of the curve described for the *Asfc* measure. Surfaces dominated by large pits with an absence of fine scratches or less wear at very fine scales, and/or more wear features at coarser scales, might have a high *Smc*.

Anisotropy (*epLsar*): measures the degree of directionality in surface roughness at a fine scale. Surfaces dominated by scratches all running in the same direction would have high *epLsar* values.

Textural fill volume (*Tfv*): examines summed volumes of square cuboids of a given scale that fill the studied surface, removing the structure of the overall surface (e.g. facet curvature), and limiting characterization to the microwear features themselves. A surface dominated with more features in the mid-scale range would have higher *Tfv* values.

Heterogeneity of complexity or heterogeneity of area-scale fractal complexity (*HAsfc*): reflects complexity variability across the surface. More heterogeneous surfaces (with higher *HAsfc* values) would have higher degree of variability in surface texture. This variable was calculated following the procedures described by El Zaatari and colleagues (2011).

Characterization of diet of El Sidrón

In order to characterize the diet of the El Sidrón adults, a comparison between Asfc and epLsar variables from other specimens of this group were used. Asfc and epLsar have been described as the most useful variables to distinguish dietary patterns between close-related species (Scott et al., 2006; Ungar et al., 2010). The samples selected for comparisons are other Neandertals grouped by vegetation cover. The data for the open-steppe and mixed environments come from El Zaatari and colleagues (2011), and the data for the wooded environment were recalculated from the data from these authors, as well as Hlusko and colleagues (2013). In addition, four extant species of known diet and microwear signatures were included for comparative porpoises: *Gorilla gorilla* and *G. beringei*, mainly herbivorous (Scott et al., 2012), and *Canis latrans* and *Lycaon pictus* mainly carnivorous (Ungar et al., 2010).

Due to the small sample size of Cueva de la Paloma sample, no statistical analyses were done. However, the sample was used on the epLsar/Asfc comparison.

Statistical analyses to test intra-group variability

Statistical analyses were performed to determine both the diet and the extent of variation within the groups.

A Mann-Whitney U test with "sex" as the grouping factor. This non-parametric analysis was chosen because data do not follow a normal distribution (Scott et al., 2006), and sample is small.

To test intra-group variability within the Indian Knoll sample, single-classification ANOVAs for each variable and multiple comparisons tests were used to determine the sources of significant variation. Fisher's LSD a priori tests and Tukey's HSD post hoc tests were run to balance risks of Type I and Type II errors (Cook and Farewell, 1996). All data were rank-transformed before analysis, in order to follow the assumptions associated with parametric statistical tests (Conover and Iman, 1981).

Results

Raw data for the five variables analyzed on the three samples are presented in Table 1, and the microwear texture surfaces are illustrated in Figure 1.

In comparison to the Neandertals grouped by ecogeographic regions and the four extant species, the El Sidrón Neandertals have, on average, higher values than the samples considered. The Asfc values of three El Sidrón individuals are closer to the carnivores than to other Neandertals (Figure 2), whereas three of them remain close to the Neandertal group.

The Mann-Whitney U test results indicate no significant sex-related differences in microwear signatures for the El Sidrón sample (Table 2)

The ANOVA results indicate no significant sex-related differences in microwear signatures for the Knoll sample (Table 3), as well as the pairwise comparisons tests.

Discussion and conclusions

In general, the Phase II surfaces analyzed in the Neandertal sample are complex, covered with features of different sizes and shapes, with random large striations and moderate pits. Surface complexity (*Asfc*) has been considered the most useful variable among all the microwear texture variables to distinguish dietary differences in Neandertals and other Hunter-gatherer groups (El Zaatari et al., 2011; Harvati et al., 2013), thus it was selected for comparisons, along with the anisotropy (epLsar), the other variable must useful (Scott et al., 2006).

Microwear texture variables are significantly correlated to the ethnographically documented or archeologically inferred differences in the diets of recent hunter-gatherer (El Zaatari, 2010, 2014; El Zaatari et al., 2011), and in particular the surface complexity variable.

The Asfc values of three El Sidrón individuals are higher than the values from other Neandertals (Figure 2), indicating that these Neandertals had a more abrasive diet than other individuals. In addition, two of the three specimens from El Sidrón site that show the highest values of Asfc from the whole sample, have been identified as females (El Sidrón Adult 3 and El Sidrón Adult 4), and the other specimen (El Sidrón Adult 7) remains with sex unknown. The remaining three specimens from El Sidrón site were identified as males, and appear to be close to the Neandertal pool, indicating a possible shift between males and females on the sample, that deserves further consideration.

However, the statistical tests reveal no sex-related differences in both the El Sidrón and Indian Knoll samples. The same lack of evidence has been found on the Ipiutak and the Tigara populations (El Zaatari, 2014). It is possible that the short-term resolution of occlusal microwear (Grine, 1986) was not able to record the dietary differences expected between males and females in all hunter-gather groups (Speth and Spielmann, 1983; Berbesque et al., 2012).

Several studies (El Zaatari, 2010, 2014; Pontzer et al., 2011; Ungar et al., 2010; El Zaatari et al., 2011; El Zaatari and Hublin, 2014) have linked high values of surface complexity to a more abrasive diet or to harder food: environmental abrasives such as sand and grit that get glued to the food items as a result of food preparation techniques, and leave marks on the enamel surface. As an example, the Tigara population was known to ingest very high amounts of environmental abrasives, and had a very high complexity average value compared with other groups (El Zaatari, 2010).

Despite not showing significant differences, women from El Sidrón sample had a diet more abrasive than males, and since a sexual division of labor has been demonstrated on this group (Estalrrich and Rosas, accepted), it could

be possible that the differential use of their mouth in other activities than the mastication itself, could be responsible of the high Asfc values detected.

The anisotropy (epLsar) values of the El Sidrón individuals have been found to be within the Neandertal range, and since this variable has been positively correlated with the level of consumption of tough items, such as vegetables (Scott et al., 2006; Ungar et al., 2012), it could be inferred that this group included such items on their dietary basis. This result is supported by the presence of starchy granules on their dental calculus (Hardy et al., 2012), indicating plant food consumption.

Another noticeable result is that the value for the Scale of maximum complexity (*Smc*) obtained for the individual El Sidrón-Adult 2 exceeds the values of the rest of the sample here analyzed. It also exceeds the values obtained for the other Neandertals reported in the literature (El Zaatari et al., 2011; Hlusko et al., 2013). This value of 10.92 is the highest ever obtained for a Neandertal (El Zaatari et al., 2011; Hlusko et al., 2013), even for Upper Paleolithic Modern Humans (El Zaatari and Hublin, 2014), with the exception of the Barma Grande 2 individual, who has a Smc value of 262.147 indicating a surface dominated by few large pits. As El Zaatari and Hublin (2014) noted, a possible explanation of the atypical values of Barma Grande 2 is that it could be the result from a single ingestion of a relatively large, abrasive item. It is possible that the same happened in the case of the El Sidrón Adult 2 individual. Another possibility is that the abrasive item was not intended to be ingested, but rather may point to the use of the mouth for other activities. Since this individual is the only one from the group who had bitumen in their dental calculus (Hardy et al., 2012), and a peculiar pattern of chipped enamel on the anterior dentition (Estalrrich et al., 2013; Estalrrich and Rosas, accepted JHE), this anomaly could be related to stone tool hafting, using molar teeth as reinforcement, causing the microwear texture to indicate hafting traces.

In sum, despite sample size, dietary differences seem to underlie the microwear texture signatures of the El Sidrón cave and Cueva de la Paloma Paleolithic sites. Further research is needed in order to clarify is these Paleolithic peoples had the same food sharing and partition behavioral patterns as modern hunter-gatherers have (Sealy, 2006; Marlowe, 2007; Berbesque et al., 2011, 2012; El Zaatari, 2014; El Zaatari and Hublin, 2014).

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Figure and Table captions

Figure 1. Three-dimensional axiomatic representations of some microwear surfaces for the El Sidrón, Magdalenian Cueva de la Paloma, and Indian Knoll samples.

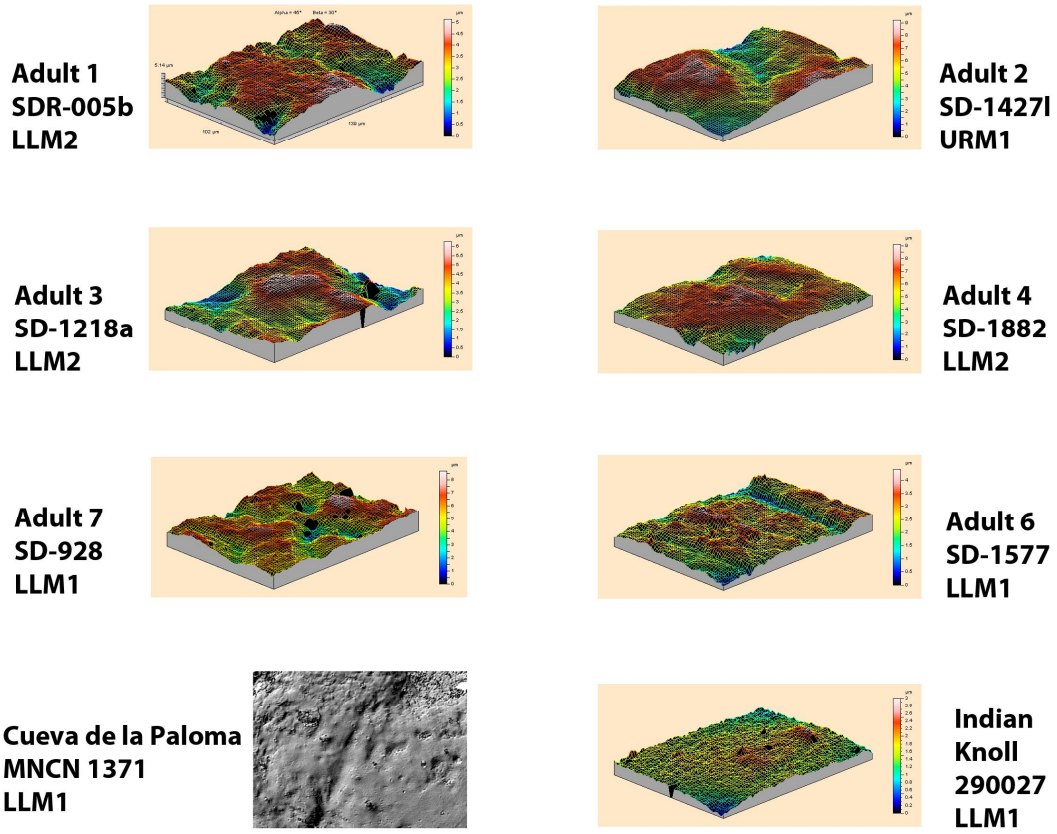
Figure 2. Bivariate plot of complexity (Asfc) vs. anisotropy (epLsar) for the Middle and Upper Paleolithic samples and the four etant species.

Table 1. Raw dental microwear texture data for the individuals from El Sidrón cave, Cueva de la Paloma, and Indian Knoll.

Table 2. Mann-Whitney U test results for the El Sidrón sample.

Table 3. One-factor ANOVA results for the variables from the Knoll sample.

Figura 1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Adult 2
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URM1
Adult 3
SD-1218a
LLM2
Adult 4
SD-1882
LLM2
Adult 7
SD-928
LLM1
Adult 6
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LLM1
Indian
Knoll
290027
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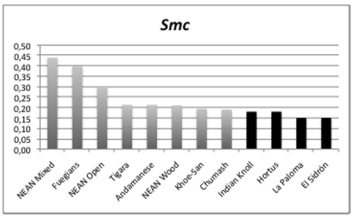
Figure 2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NEAN Wood
Khoe-San
Chumash
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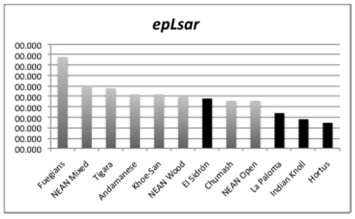
Hortus
La Paloma
El Sidrón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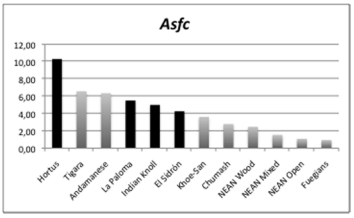
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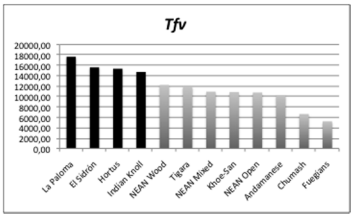
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Fuegians

Table 1.

Specimen	Tooth/Facet	Asfc	epLsar	Smc	Tfv	HAsfc	Sex	Age
El Sidrón cave (Asturias. Spain). *Homo neanderthalensis*.								
SDR-005b	LLM2 / facet 9	3.34	0.0024	0.15	17271.63	0.16	Male	Adult
SD-1427l	URM1/ facet 9	1.49	0.0029	10.92	17157.75	0.38	Male	Adult
SD-1218a	LLM2 / facet 9	5.28	0.0037	0.15	14122.39	0.31	Female	Adult
SD-1882	LLM2 / facet 9	6.11	0.0017	0.15	16072.48	0.21	Female	Adult
SD-1577	LLM1 / facet 9	4.02	0.0025	0.15	15554.58	0.18	Male	Adult
SD-928	LLM2 / facet 9	5.73	0.0010	0.15	12813.98	0.20	Unknown	Adult
Cueva de la Paloma (Asturias. Spain). *Homo sapiens*.								
MNCN1364-5	LRM2 / facet 9	5.24	0.0016	0.15	22029.60	0.10	Female	Adult
MNCN1366	LRM2 / facet 9	2.05	0.0027	0.15	16266.32	0.17	Female	Adult
MNCN1371	LLM2 / facet 9	4.81	0.0013	0.15	14047.94	0.33	Male	Adult
Indian Knoll (Kentucky. USA). *Homo sapiens*.								
290081	URM1 / facet 9	3.61	0.0008	0.21	13360.66	0.10	Female	Adult
290078	LLM1 / facet 10n	3.94	0.0016	0.27	18941.32	0.09	Female	Adult
290077	LLM1 / facet 9	5.36	0.0010	0.15	13285.66	0.10	Female	Adult
290076	URM1 / facet 9	5.92	0.0009	0.15	10445.39	0.26	Male	Adult
290070	LLM2 / facet 10n	6.25	0.0020	0.15	16363.37	0.03	Male	Adult
290063	URM2 / facet x	3.43	0.0014	0.15	14786.73	0.08	Female	Adult
290061	URM2 / facet 9	5.58	0.0010	0.15	15392.17	0.07	Male	Adult
290057	LRM2 / facet 9	5.85	0.0003	0.15	10921.29	0.11	Male	Adult

290052	ULM2 / facet 9	3.72	0.0014	0.15	16526.42	0.16	Male	Adult
290049	LRM2 / facet 9	3.30	0.0028	0.15	12279.10	0.21	Female	Adult
290042	URM1 / facet 9	5.16	0.0018	0.15	12159.87	0.11	Male	Adult
290040	URM1 / facet 9	3.16	0.0013	0.34	9309.99	0.01	Male	Adult
290039	LRM2 / facet 9	6.10	0.0006	0.34	14221.87	0.12	Male	Adult
290038	LRM2 / facet 9	10.33	0.0005	0.15	17185.35	0.06	Male	Adult
290036	ULM2 / facet 9	2.57	0.0016	0.27	20521.85	0.18	Male	Adult
290035	LRM1 / facet 10n	5.85	0.0019	0.15	15702.84	0.21	Male	Adult
290034	LRM2 / facet 9	1.33	0.0007	0.15	18321.54	0.05	Female	Adult
290033	URM2 / facet 9	2.49	0.0025	0.15	7938.89	0.09	Female	Adult
290028	ULM2 / facet 9	6.70	0.0015	0.15	17047.87	0.08	Female	Adult
290025	URM2 / facet 10n	4.32	0.0016	0.15	15865.49	0.05	Male	Adult
290024	LRM2 / facet 9	5.73	0.0014	0.15	12839.57	0.08	Female	Adult
290022	LRM1 / facet x	1.85	0.0009	0.27	13516.40	0.06	Female	Adult
290021	LLM2 / facet 9	3.79	0.0015	0.15	20412.99	0.06	Male	Adult
290019	LRM1 / facet 9	7.48	0.0016	0.15	13047.33	0.01	Female	Adult
290006	URM1 / facet x	7.91	0.0010	0.15	11349.42	0.05	Female	Adult

Table 2.

Mann-Whitney U Test (All data for Stat new analysis) By variable Sex Marked tests are significant at p

	Rank Sum - male	Rank Sum - female	U	Z	p-value	Z - adjusted	p-value	Valid N - male	Valid N - female	2*1sided - exact p
Asfc	6.00000	9.000000	0.000000	-1.44338	0.148916	-1.44338	0.148916	3	2	0.200000
epLsar	9.00000	6.000000	3.000000	0.28868	0.772830	0.28868	0.772830	3	2	1.000000
Tfv	11.00000	4.000000	1.000000	0.86603	0.386477	0.86603	0.386477	3	2	0.400000
1x1 HAsfc	8.00000	7.000000	2.000000	-0.28868	0.772830	-0.28868	0.772830	3	2	0.800000

Table 3.

Test of SS Whole Model vs. SS Residual (Sex HG) Include cases: 56:85											
	Multiple - R	**Multiple - R²**	**Adjusted - R²**	**SS - Model**	**df - Model**	**MS - Model**	**SS - Residual**	**df - Residual**	**MS - Residual**	**F**	**p**
Asfc	0.091758	0.008420	-0.026994	104.0024	1	104.0024	12248.46	28	437.4452	0.237750	0.629632
epLsar	0.076233	0.005811	-0.029695	55.7357	1	55.7357	9534.96	28	340.5344	0.163671	0.688873
Smc	0.068181	0.004649	-0.030900	58.3149	1	58.3149	12486.03	28	445.9295	0.130772	0.720348
Tfv	0.146137	0.021356	-0.013596	327.7167	1	327.7167	15017.75	28	536.3482	0.611015	0.440966
HAsfc 1x1	0.075922	0.005764	-0.029744	53.5714	1	53.5714	9240.43	28	330.0153	0.162330	0.690080

CAPÍTULO VIII - DISCUSIÓN GENERAL

Como se ha comentado en la introducción de esta tesis, la variabilidad humana depende de la relación entre el ambiente cultural, el ambiente físico y la biota que lo acompaña. Es esta tesis se ha planteado indagar en la variabilidad del comportamiento biocultural de *Homo neanderthalensis*. En los capítulos anteriores se han presentado una serie de resultados sobre el desgaste dental en Neandertales, y las implicaciones que la variabilidad observada entre los individuos puede tener en el comportamiento de esta especie extinta, se discutirá a continuación.

Diferentes estudios han probado que los Neandertales tenían un modo de vida similar a los grupos de cazadores-recolectores actuales. Eran excelentes cazadores de presas de tamaño medio y grande, a veces incluso se especializaban en un tipo de presa, y eran principalmente carnívoros (Gaudzinski y Roebroeks, 2000; Hoffecker y Cleghorn, 2000; Patou-Matis, 2000; Richards *et al*., 2000; Bar-Yosef, 2004; Bocheners *et al*., 2005). Además, también utilizaban otros recursos alimenticios, como presas pequeñas, animales de origen marino, diversos vegetales y tubérculos, y también tenían un buen conocimiento y manejo del fuego y cocinaban su comida (Stringer *et al*., 2008; Henry *et al*., 2011; Blasco y Fernández-Peris, 2012; Hardy *et al*., 2012).

Como sociedades de cazadores-recolectores, se espera que tengan la misma organización social y estrategias de supervivencia que los cazadores-

recolectores actuales, lo que implica una separación o división del trabajo entre los sexos dentro del grupo, que en un momento se sustentó con el estudio del grosor de la tibia en una muestra Neandertal (Ruff, 1987). Sin embargo, la falta de evidencias de actividades específicas de las mujeres cazadoras- recolectoras (como las herramientas líticas apropiadas para triturar o moler vegetales), indican que los Neandertales no debieron tener esta extrema especialización entre los sexos, al menos en cuanto al aprovisionamiento de comida se refiere, y que tanto hombre como mujeres participaban de las mismas actividades de caza (Kuhn y Stiner, 2006; Blasco y Fernández-Peris, 2012; Cochard *et al*., 2012). Pero todavía queda una pregunta importante por resolver. ¿Qué ocurre después del aprovisionamiento de la comida? ¿Qué hacían? ¿Se repartían el trabajo o todos hacían lo mismo?

El estudio del desgate dental asociado a tareas no masticatorias, así como el asociado con la dieta, ha sido capaz de revelar pautas de comportamiento en diversas poblaciones del pasado (Molnar, 1972; Merbs, 1983; Lukacs y Pastor, 1988; Molleson, 1994; Belcastro *et al*., 2004; Bonfiglioli *et al.*, 2004; Scott y Jolie, 2008; Molnar, 2008; El Zaatari *et al*., 2011; Lorkiewicz, 2011; Henry *et al*., 2012), y algunas actuales (Berbesque *et al*., 2012). Su estudio en los Neandertales de l'Hortus, Spy y el grupo familiar de El Sidrón ha revelado algunos datos sobre el comportamiento de esta especie extinta, más allá del aprovisionamiento de la comida.

Se ha encontrado que las mujeres presentan más estrías culturales y más largas que los hombres, y la distribución de mellas en el esmalte dental es también distinta: más abundante en la dentición maxilar de los hombres y en la

dentición mandibular de las mujeres. Estos resultados que existen diferencias entre hombres y mujeres, indicando una división sexual del trabajo entre los individuos Neandertales.

Ambas señales se asocian a diversos comportamientos. Por ejemplo, las mellas en el esmalte se han asociado al uso de la dentición en el retoque de herramientas líticas en los hombres Aborígenes australianos (Gould, 1968), o en las mujeres Inuit de la isla de Groenlandia debido a que se ayudaban de sus dientes durante la manufactura de ropa (Scott y Jolie, 2008). También se ha descrito en diversas poblaciones Neandertales (de Lumley, 1973; Wallace, 1975; Garralda y Vandermeersch, 2000; Tillier *et al*., 2003; Fiorenza, 2009; Lozano *et al*., 2013), y los datos aquí obtenidos contribuyen a conocer cómo se repartía esta acción entre los individuos de un grupo.

Las estrías culturales se han descrito abundantemente en Neandertales (Martin, 1923; de Lumley, 1973; Trinkaus, 1983; Bermúdez de Castro *et al*., 1988; Lalueza-Fox y Frayer, 1997; Frayer *et al*., 2010; Volpato *et al*., 2012; Estalrrich y Rosas, 2013) y se han relacionado con un comportamiento llamado “stuff-and-cut” (Molnar, 1972), o "sujetar y cortar". Un comportamiento extendido entre todos los miembros de los grupos Inuit consiste en que sujetan tozos de carne y cortan con un cuchillo un pequeño trozo que se van a comer (Seagrief, 1993; Wood, 1992; Faurie *et al*., 2005). Esta parece ser la causa principal atribuida a la presencia de estrías culturales en Neandertales y otros homininos del Pleistoceno (de Lumley, 1973; Trinkaus, 1983; Bermúdez de Castro *et al*., 1988; Lalueza-Fox y Frayer, 1997; Lozano *et al*., 2004).

Algunas de las actividades responsables de estas diferencias pueden ser el raspado o preparación de pieles, rasgado y fabricación de tendones para hacer cordones y manufactura de ropa, que en sociedades cazadoras-recolectoras está generalmente asociado a las tareas femeninas (Merbs, 1968; Murdock y Provost, 1973; Ryan y Johanson, 1989). En hombres se ha visto que suelen utilizar la dentición a modo de pinza (herramienta que no suelen tener), o para sujetar otras herramientas como taladros y agujas y poder tener las manos libres para otras actividades (Merbs, 1968; Lucaks y Pastor, 1988).

A partir de estos comportamientos, y con los datos obtenidos en esta tesis, se extrapola un posible comportamiento de los Neandertales. Tanto hombres como mujeres, adultos y niños, utilizaban la dentición en diferentes actividades, en las que todos usaban el mismo tipo de herramientas líticas, pero con diferencias en la tarea que realizaban. Dado que los hombres tienen un patrón más marcado de mellas en la dentición maxilar, que se asocia a actividades que requieren una gran fuerza o presión puntual que pueden romper el esmalte dental, se propone que los hombres fueran los encargados de utilizar su boca como una pinza, y de retocar el filo de las herramientas líticas que utilizaban, mientras que la presencia de más estrías culturales y más largas en las mujeres indica que realizaban más tareas de cortar materiales que los hombres, lo que puede indicar que se encargaban de la preparación de pieles y fabricación de ropa, señalando un comportamiento muy similar al de las sociedades-cazadoras actuales.

Además, el estudio del microdesgaste en los molares de los individuos adultos de El Sidrón ha señalado que, aunque no hay diferencias

estadísticamente significativas entre ellos, los hombres y las mujeres de El Sidrón se distribuyen de manera separada cuando se consideran las variables de complejidad (Asfc) y anisotropía (epLsar), que han demostrado ser útiles a la hora de distinguir la dieta entre especies e incluso entre individuos (Scott *et al*., 2005, 2006; Merceron *et al*., 2010). Las muestras de cazadores-recolectores analizadas (Cueva de la Paloma e Indian Knoll) tampoco han mostrado diferencias entre hombres y mujeres. En el caso de la cueva de La Paloma la muestra analizada es muy pequeña (un hombre y dos mujeres) insuficiente para realizar tests estadísticos con fiabilidad. En el caso de la colección Indian Knoll, los resultados estadísticos tampoco han mostrado diferencias entre ambos sexos, lo cual puede deberse a la propia historia de los restos humanos. La ensenada donde está el yacimiento era ocupada estacionalmente por un grupo de Paleo-Indios (Webb, 1974). Es posible que estas ocupaciones estacionales sucesivas y a lo largo del tiempo enmascaren las diferencias que pudiera haber entre hombres y mujeres, ya que al tratarse de grupos distintos de una misma población, las variaciones intergrupales pueden ser más evidentes que las diferencias intragrupales entre los hombres y las mujeres.

Sin embargo, las 2 mujeres y el adulto sin sexo definido de la muestra de El Sidrón tienen la superficie oclusal más compleja que los 3 hombres del grupo, aunque todo el grupo presenta similitud a la de las especies carnívoras incluidas en el análisis, indicando una dieta más carnívora en las últimas semanas de vida. Altos valores de complejidad también se han obtenido en el grupo de cazadores-recolectores Tigara y Andamaneses, debido a que junto a su comida, introducían pequeñas partículas abrasivas como granos de arena (El Zaatari, 2010),

indicando que en grupos similares con una dieta similar, los factores de preparación de la comida u otros de origen también cultural afectan a la complejidad de la superficie. Recientemente, El Zaatari (2014) ha analizado la superficie oclusal de los grupos Ipiutak y Tigara de Point Hope (Alaska), mostrando que los individuos de mayor edad los que presentan más evidencias de que el desgaste masticatorio esté afectado por el desgaste no masticatorio . El hecho de que las mujeres tengan unos valores más altos en la variable Asfc, puede indicar que las mujeres de este grupo incluían más abrasivos en la dieta, y apoyando a lo comentado en el párrafo anterior, debido a que se ayudaban con la boca a preparar las pieles para hacer ropa. Las pieles utilizadas reposarían en el suelo, y al sujetarlas con la boca, las partículas de arena que estuvieran pegadas, también se introducirían en la boca, erosionando y camuflando la textura de la superficie creada exclusivamente por las propiedades de fractura de la comida. Se ha hallado en su sarro compuestos químicos asociados a plantas medicinales de sabor amargo (posiblemente *Chamaemelum nobile* y *Achillea millefolium*) y pigmentos. Es posible que, junto a su uso medicinal, quizás también hayan sido empleados para curtir pieles ya que estas plantas tienen taninos en su composición (Ashok y Upadhyaya, 2012).

Otro resultado importante que hay que destacar es la exclusividad en el comportamiento biocultural detectada en el individuo El Sidrón Adulto 2 en cada rasgo del desgaste dental estudiado. Aunque los resultados indican que el individuo era diestro, lo cierto es que la últimas estrías que se produjo fueron hechas con su mano izquierda. Este individuo tiene una severa patología oral (Prieto, 2005; Dean *et al*., 2013) en el lado izquierdo de su mandíbula, y tiene

grandes depósitos de cálculo dental en la superficie oclusal de sus molares izquierdos, tanto mandibulares como maxilares, señal de que no masticaba con su lado izquierdo, posiblemente para evitar el dolor, y que muy probablemente incluso sujetar materiales ayudado con el lado izquierdo de su boca debía ser doloroso, por lo que se ha propuesto que para continuar con sus tareas habituales, este individuo cambió el lado de la boca con el que sujetaba los materiales (ahora sería el derecho) y que por tanto, comenzó a utilizar su mano izquierda para cortar los materiales, de otra manera hubiera sido probable que se cortara la cara. Además, este es el único individuo que presenta toda su dentición anterior llena de melladuras, con un aspecto festoneado, conocido como "nibbling effect" (Scott y Winn, 2011), y en su sarro se han detectado trazas de bitumen (Hardy *et al*., 2012), usado a modo de pegamento para unir puntas a las lanzas y flechas (Boëda *et al.,* 1996) durante el Paleolítico medio. El estudio del microdesgaste oclusal, también corrobora la peculiaridad de este individuo, puesto que es el único de la muestra analizada que tiene un valor tan elevado en la variable *Smc*, que indica que el individuo masticó algún material altamente abrasivo, como ha sido sugerido en un individuo del Paleolítico superior (El Zaatari y Hublin, 2014). La unión de todos estos datos hace pensar que este individuo se ayudaba de su boca cuando estaba haciendo lanzas o enmangando piezas líticas, y que al hacerlo, además de dejar trazas de bitumen en su sarro, produjo pequeñas fracturas en su esmalte dental, y que debido a una patología dental, fue capaz de desarrollar la capacidad de utilizar con la misma habilidad la mano izquierda que la derecha. Todas estas evidencias sustentan un comportamiento especial y único de este hombre, que no ha sido observado antes en ningún individuo Neandertal. La originalidad de este individuo radica

en el hecho de que participara en muchas actividades de un modo en las que ningún otro individuo analizado lo hacía, y le confiere un carácter especial. El hecho de que haya sido el único individuo al que se le ha encontrado rastros de bitumen y el patrón festoneado de su dentición maxilar induce a pensar que era el único individuo de su grupo que se ocupaba de enmangar la industria lítica. En cuanto al estudio de la lateralidad manual, los Neandertales de El Sidrón eran diestros, con el mismo patrón actual de lateralidad manual (Faurie *et al*., 2005), y aportan evidencias indirectas acerca de la lateralización del cerebro en Neandertales, que junto con las asimetrías en los senos venosos (Peña-Melián *et al*., 2011), la morfología del hueso hioides (Rodríguez *et al*., 2003) o la presencia de la misma variante del gen FOXP2 (Krause *et al*., 2007) como parte de la base que permite la capacidad de habla humano, refuerzan la noción de que los Neandertales poseían un patrón moderno de asimetría cerebral, que a su vez encaja con los patrones de comportamientos bioculturales descritos, similares a los de sociedades cazadoras-recolectoras actuales e incitan a pensar también en capacidades cognitivas similares.

El individuo El Sidrón Juvenil 1 muestra el mismo patrón de lateralidad manual que los adultos de la muestra. Hasta ahora siempre se había estudiado la lateralidad manual en Neandertales sólo en individuos adultos, siendo esta es la primera vez que se hace en un individuo juvenil. La edad estimada para este individuo es de unos 7,5 años de edad (Rosas et al., in prep.), indicando que a esa edad los Neandertales ya tenían establecida su lateralidad manual como en los humanos actuales. En nuestra especie, el uso unimanual para alcanzar o agarrar objetos se ha detectado muy temprano en bebés, incluso durante el desarrollo

embrionario (Nelson *et al*., 2013), aunque la preferencia manual cuando se desarrollan tareas más complejas y acciones bimanuales, suele aparecer más tarde, y se establece completamente en torno a los 7 años de edad (Fennell, 1986; Sacrey *et al*., 2012). Dado que tanto el número de estrías culturales es ligeramente menor que en los adultos (señal de que este individuo realizó la acción menos frecuentemente que los demás, como han sugerido Bermúdez de Castro *et al*. (1988) y Lozano *et al*. (2008) para individuos inmaduros del Pleistoceno medio) y su morfología es ligeramente curvada, puede ser posible que este individuo utilizara su dentición para sujetar y cortar pedazos de carne para comer (como el resto de individuos), a la vez que estuviera aprendiendo como usar su boca como una tercera mano, y como ocurre en las sociedades de cazadores-recolectores actuales, es en la etapa juvenil cuando los individuos aprenden los comportamientos adultos (Bogin, 1999; Marlowe, 2005; Hewlett *et al*., 2011).

Varios estudios y proyectos se están llevando a cabo para conocer mejor el comportamiento de esta especie. Como ya se ha mencionado en la Introducción, hoy sabemos que los Neandertales poseían un excelente conocimiento del medio en el que vivían (El Zaatari *et al*., 2011; Henry *et al*., 2011; Hardy *et al*., 2012), fueron capaces de cambiar su cultura material con el tiempo e introdujeron elementos simbólicos (Bailey y Hublin, 2006; Caron *et al*., 2011; Hublin *et al*., 2012), utilizaban pigmentos y plumas (Soressi y d'Errico, 2007; d'Errico *et al*., 2010; Zilhão *et al*., 2010; Roebroeks *et al*., 2012) y enterraban a sus muertos (Gargett, 1989, 1999; Rendu *et al*., 2014), que lleva asociado también un comportamiento simbólico. La complejidad del

comportamiento de los Neandertales se va mostrando cada vez mayor: ordenaban los abrigos en los que vivían según las actividades que desarrollaban (Vallverdú *et al*., 2010, 2012; Rosell *et al*., 2012), uso del entorno (Daujeard y Moncel, 2010), y el uso de plantas medicinales y bitumen (Hardy *et al*., 2012). Y es en este entorno donde los resultados aquí presentados se engloban. Aportan nuevas evidencias respecto al comportamiento biocultural de los Neandertales, mediante el estudio de los rasgos de desgaste dental asociado a diversas actividades, y sus resultados permiten incrementar el paradigma de la organización social de los Neandertales, mostrando que era parecida a la que conocemos en grupos actuales, permitiendo vislumbrar que la aparición de comportamiento que reconocemos como moderno, era más compartido con la especie *Homo neanderthalensis* de lo que en principio podría parecer.

CAPÍTULO IX - CONCLUSIONES

El objetivo principal de esta tesis ha sido conocer los comportamientos bioculturales asociados a *Homo neanderthalensis* según la edad y el sexo a partir del análisis del desgaste dental. Así, se han llegado a las siguientes conclusiones:

1. Se han obtenido evidencias de una división sexual del trabajo en los grupos Neandertales en las tareas posteriores a la adquisición de los alimentos, a través del estudio del desgaste dental para-masticatorio.

2. Las mujeres Neandertales pudieron realizar más actividades relacionadas con el raspado y preparación de pieles, mientras que las actividades de los hombres pudieron estar relacionadas con el retoque del filo de herramientas líticas.

3. No se han encontrado diferencias entre Neandertales adultos, adolescentes y juveniles, indicando que todos los individuos utilizaban su boca en actividades no masticatorias.

4. El estudio de la lateralidad manual en los Neandertales de El Sidrón ha demostrado que comparten el mismo patrón que *Homo sapiens*, siendo un grupo mayoritariamente diestro.

5. No se han encontrado diferencias en los rasgos del microdesgaste entre individuos adultos masculinos y femeninos en ninguno de los grupos estudiados (Neandertales de El Sidrón, *H. sapiens* de Cueva de la Paloma e Indian Knoll).

En relación más directa con el grupo de neandertales de El Sidron se han obtenido también las siguientes conclusiones.

6. Se han identificación y caracterizado 13 individuos en el yacimiento Neandertal de la cueva de El Sidrón: siete individuos adultos (tres hombres, tres mujeres, uno indeterminado), tres individuos adolescentes (dos hombres, una posible mujer), dos juveniles (uno masculino, uno indeterminado), un individuo infantil de sexo indeterminado.

7. El estudio de los surcos subverticales en las facetas interproximales de los dientes ha resultado esencial en la asociación de dientes aislados.

8. El individuo El Sidrón Adulto 2 presenta un comportamiento especial y diferenciado en su grupo, no observado en ningún otro Neandertal estudiado en esta tesis. Las evidencias apuntan a que usaba su boca para ayudarse a enmangar piezas líticas.

9. El individuo El Sidrón Adulto 2 cambió el uso de la mano derecha por la izquierda debido a una patología oral en el lado izquierdo de su mandíbula.

10. El individuo El Sidrón Juvenil 1 parecía estar aprendiendo los comportamientos adultos, compartiendo el mismo patrón de desarrollo de la lateralidad manual que los humanos actuales.

11. El estudio del microdesgaste dental relacionado con la dieta revela que los individuos adultos de la cueva de El Sidrón tuvieron una dieta más carnívora que los Neandertales de ambientes similares.

12. Las mujeres Neandertales de El Sidrón tienen evidencias de haber masticado materiales más abrasivos que los hombres, siendo posible que estos materiales sean las pieles que preparaban para hacer ropa, como se

ha evidenciado en las mujeres de diversos grupos cazadores-recolectores actuales.

13. Las mujeres Neandertales de El Sidrón presentan compuestos químicos provenientes de plantas medicinales en su sarro que, además de como uso medicinal, quizás también hayan empleado como taninos para el curtido de pieles.

CAPÍTULO X – BIBLIOGRAFÍA

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